The ecology of the Tekapo ground wētā (*Hemiandrus* new sp.; Orthoptera: Anostostomatidae) and recommendations for the conservation of a threatened close relative.

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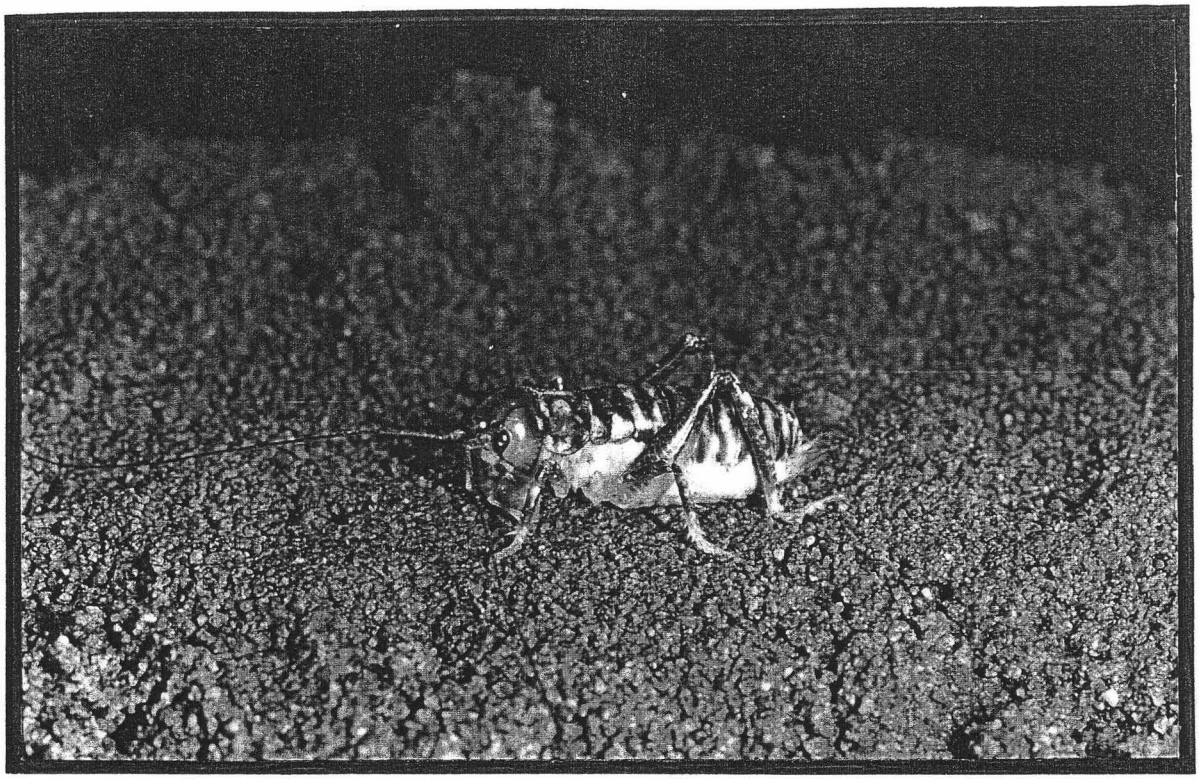
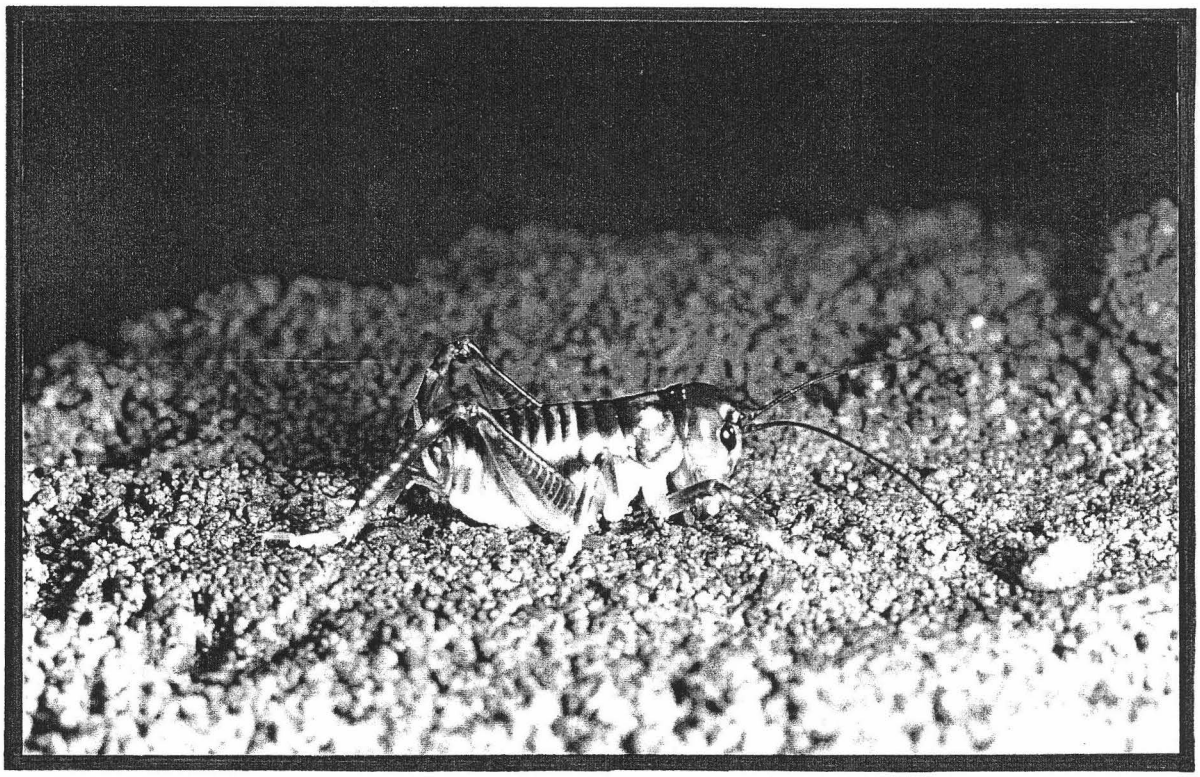


Adult female Tekapo ground wētā (*Hemiandrus* new sp.).



Adult male Tekapo ground wētā (*Hemiandrus* new sp.).

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Abstract

At a few sites near Cromwell and Alexandra, Central Otago, there exist isolated populations of a threatened ground wētā (*Hemiandrus* sp.). Research was required to establish guidelines for a management programme to enhance the species' chances of long term survival. To avoid disturbance of the threatened species, a newly discovered, relatively widespread and abundant allopatric species (*Hemiandrus* new sp. from the Tekapo River area) was selected for study. A sixteen month sampling programme based on pitfall trapping was employed to characterise the species' distribution relative to habitat variables. By far the most important determinant of distribution was the local depth of substrate available for burrowing, wētā being most abundant where friable silty soil was deepest. Female wētā oviposit in their own burrows in late summer, and the eggs hatch in the following spring. Over two years, female nymphs develop through nine instars, and males ten. Males die soon after mating in their third summer, while females overwinter with their eggs, surviving until the following summer. Analysis of the crop contents of a sample of wētā revealed that the species is a primarily herbivorous omnivore. Wētā caught in summer were significantly more herbivorous than those caught in the other seasons. *Hemiandrus* new sp. constructs its burrows in silty loam, and closes the top with a cap or plug. At the lower end of the burrow is a slightly enlarged chamber curved nearly horizontal. The most serious current predators of the Tekapo wētā, apart from native invertebrates, are hedgehogs and cats. It was considered reasonable to extrapolate conclusions about the Tekapo species regarding habitat requirements, life history and potential threats to the remaining populations, to the Cromwell species. Recommendations for the management of the Cromwell species (and other closely related threatened species) based on the conclusions of the research are presented, as well as suggestions for important further work.

Chapter 1
General Introduction

The New Zealand insects referred to as wētā are members of the worldwide order Orthoptera. They are flightless, largely nocturnal and form a distinctive part of our endemic invertebrate fauna. Strictly speaking, the term wētā as Māori originally used it applies to the ground, tree and giant wētā (Anostostomatidae)[1] (Salmon, 1955). However, the word has come to mean these taxa plus the cave wētā (Rhaphidophoridae), known to Māori as tokoriro (Miller, 1970).

Four genera of New Zealand Anostostomatidae are currently defined[2]. Giant wētā (*Deinacrida* spp.) are well known but rarely seen, being largely confined to islands and inaccessible mountain habitats, and comprise 11 species (seven named and four awaiting description) (Gibbs, 1994). Tree wētā (*Hemideina* spp.) are the common medium to large sized wētā often met with in forests and gardens throughout New Zealand (except Southland and parts of Otago). The genus includes six (Gibbs, 1994) or possibly seven (Gibbs and Richards, 1994) described species. The ground wētā are the most diverse of New Zealand's Anostostomatidae, with seven described and 30 undescribed species (P.M. Johns, pers. comm.). Presently they are divided into two genera: those with long ovipositors (*Zealandosandrus* spp.) and those with short ones (*Hemiandrus* spp.). As there are some ground wētā with an ovipositor of intermediate length the two genera should be united, but have not been formally synonymised (P.M. Johns, pers. comm.). In this work the name *Hemiandrus* refers to all ground wētā, unless otherwise stated. *Hemiandrus* species are often (but not always) small, unspectacular wētā which burrow in the soil of forests and grasslands.

Wētā have been the subjects of scientific papers since the 1840s, but only in the past four decades has anything more than a passing interest in topics other than taxonomy been taken. While considerable research has been undertaken on many aspects of the biology of tree wētā and giant wētā, little has been published on the ground wētā. The only in-depth works available are Wahid (1978) on *Hemiandrus* sp. from Banks Peninsula, Cary (1981) on *Zealandosandrus gracilis* from Canterbury beech forests and Butts (1983) on *Z. subantarcticus* from Snares Island.

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[1]Since the 1950s, it has been generally accepted that the New Zealand ground, tree and giant wētā belong to the Stenopelmatidae Burmeister 1838, a family found principally in Central America and Africa. However, based on likely evolutionary relationships between groups from different areas, P.M. Johns (University of Canterbury) considers these New Zealand wētā to belong to the Anostostomatidae Saussure 1859 (P.M. Johns, pers. comm.).

[2]This is excluding the little known tusked wētā (one described and one undescribed species), which each comprise a monospecific genus.

Background to the project.

Since the 1970s a species of *Hemiandrus* has sporadically been collected from remnant terrace and dune areas in Central Otago, mostly near the small town of Cromwell (table 1.1). Recent concern about the continued existence of the Cromwell ground wētā led to the initiation of this work, intended to establish guidelines for the management of the remaining populations. The only known substantial population of the wētā exists in the Cromwell Chafer Beetle Nature Reserve, 1.5 km south-west of Cromwell (fig. 1.1). In order to avoid undue disturbance of this very localised population, a related non-endangered allopatric species of ground wētā with what appeared to be similar habitat requirements (e.g. substrate type, vegetation, climate) was selected for study. The work involved the collection and interpretation of ecological data for the non-endangered species with the aim of applying any relevant findings in the development of recommendations for the conservation of the endangered species.

Table 1.1. Recorded collections and observations of the Cromwell wētā (*Hemiandrus* new sp.). C.C.R. refers to the Cromwell Chafer Reserve, which was not formally gazetted until 1983. Note: imm. = immature.

Date	Location	Specimens
Feb. 1974	sand dunes, Cromwell	1 imm. male
Nov. 1994	Sand Flat Rd., Cromwell	1 imm. female
Nov. 1994	Sand Flat Rd., Cromwell	1 imm. male
Mar. 1975	area of C.C.R.	1 adult male
Mar. 1975	sand flat, Cromwell	1 adult female
Mar. 1975	area of C.C.R.	1 imm. female
Mar. 1975	Pearson Rd., Cromwell	1 adult male
Feb. 1976	Alexandra	1 adult male
Nov. 1977	area of C.C.R.	2 imm. males, 1 imm. female
Nov. 1977	Dunstan Rd., north of Alexandra[4]	1 imm. female
Mar. 1979	area of C.C.R.	1 adult male
prior to 1993[3]	Brassknocker Rd., 9km north-east of Alexandra	2 (sex not stated)
Mar. 1993	C.C.R. (during D.o.C. survey)	4 (sex not stated)
Mar. 1993	Sand Flat Rd., Cromwell (during D.o.C. survey)	2 males
since 1993	C.C.R.	"many wētā" observed
since 1993	Flat Top Hill Conservation Area (south of Alexandra)	not specified

A species of ground wētā which appeared ideal for such work was discovered in 1992. During an invertebrate sampling study on and around the Tekapo River delta (South Canterbury) in December of that year, a previously unknown species of ground wētā was trapped in small numbers (Sinclair, 1995). Subsequent sampling in other areas revealed that the species is common around parts of the

[3]These specimens were collected by B. Emerson before the D.o.C. survey, but the actual dates are not available.

[4]The specimen referred to here was erroneously labelled as collected from Alexandra Tce., north of Dunstan Rd., Cromwell.

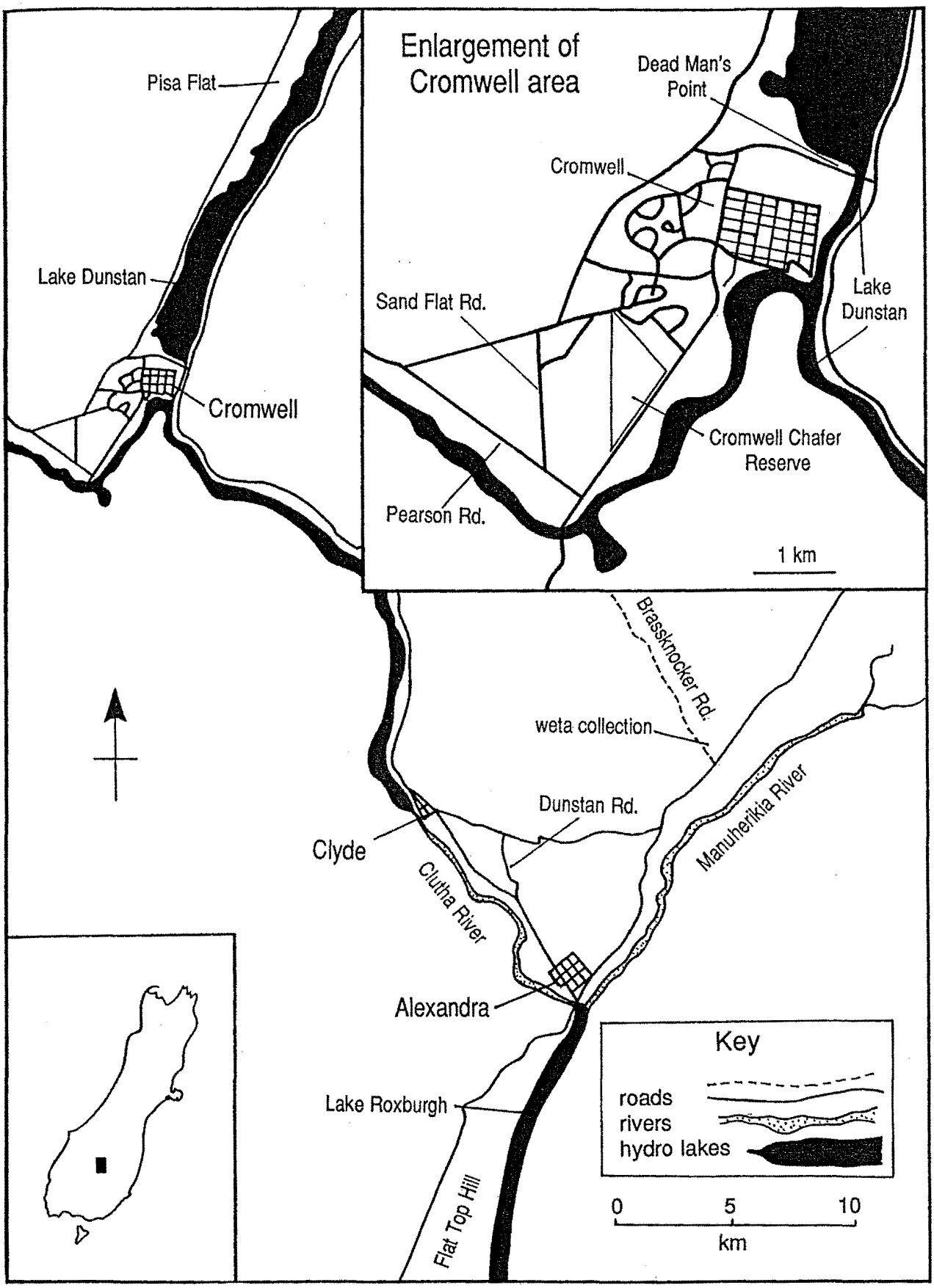

Figure 1.1. Map of the Cromwell and Alexandra region (Central Otago), indicating locations referred to in the text.

delta and for at least several kilometres northwest along the Tekapo River. The species also remains undescribed but is morphologically similar enough to be a close relative of the Cromwell *Hemiandrus* species (P.M. Johns, pers. comm.).

As there is very little information available on any aspects of ground wētā biology in New Zealand, the findings of this work on the Tekapo *Hemiandrus* sp. will contribute to the understanding of the biology of ground wētā in general.

The Cromwell Wētā.

During the 1970s the Cromwell *Hemiandrus* species was collected from at least three areas in and around Cromwell and one area in Alexandra, and since then from at least two areas around Alexandra (table 1.1). The Department of Conservation surveyed four areas potentially suitable for the Cromwell wētā in March 1993 (McKinlay and Gibson, 1993). Night-time searches of the ground were made by torch light. Four wētā were found in the Cromwell Chafer Beetle Nature Reserve and two in one other area (Sand Flat Road) (fig. 1.1). All specimens were seen on cushions of native scabweed (*Raoulia australis*). The two searched areas in which no specimens were found were probably unsuitable habitat. Dead Man's Point had a severely depleted *R. australis* population, was heavily infested with rabbits and was often disturbed by recreational motorcycling. Pisa Flat (fig. 1.1) was an undisturbed site but soils there may be too compact for the wētā to burrow in (McKinlay and Gibson, 1993).

Since this survey, staff from D.o.C. in Otago have undertaken considerable pitfall trapping on the Cromwell Chafer Reserve and caught many wētā (B. McKinlay, pers. comm.), indicating that the species is present in reasonable numbers at least in this one area. Interestingly, after a survey of another insect in the reserve (the chafer beetle *Prodontria lewisi;* see below), it was stated that the beetle shared its habitat with "common insects including ... the ground wētā *Zealandosandrus*" (Dept. of Lands and Survey, 1984). The animal referred to was undoubtedly the Cromwell *Hemiandrus* species. The wētā population on the reserve is, however, completely isolated from any others by development of surrounding land.

The Cromwell Chafer Reserve is the only sizeable area of conservation land in lowland Central Otago (Rance, 1990). Recently, however, the Cromwell wētā has been observed in two new sites; terraces of the Manuherikia River near Brassknocker Road (9 km north-east of Alexandra) (B. Emerson, pers. comm.), and the Flat Top Hill Conservation Area (south of Alexandra) (B. McKinlay, pers. comm.), indicating that remnant populations are widespread. Considerable changes to surrounding land have reduced the likelihood of populations of the wētā surviving elsewhere. Such changes include the flooding of much low-lying land, including river terraces (potential wētā habitat), by the filling of Lake Dunstan for the Clyde Hydroelectric Power Project, the relocation of flooded orchards and continuing development of Cromwell. Other land uses in the area have changed

considerably over the past two decades, with an increase of more intensive agriculture (such as orcharding, forestry and lifestyle blocks) over the traditional extensive pastoralism. Pine forestry in particular is considered to have affected potential habitats of the Cromwell wētā significantly, as the thick layer of decaying prunings and pine needles covers the existing vegetation, inhibiting its growth (McKinlay and Gibson, 1993). Much land surrounding the Cromwell Chafer Reserve is now in plantation forest. Most of these developments have occurred since the 1970s (the decade when the majority of wētā collections were made outside the Cromwell Chafer Reserve) suggesting that indeed the populations may be much reduced from previously (McKinlay and Gibson, 1993).

The reserve was formally gazetted in 1983 (Dept. of Lands and Survey, 1984) after recommendations by Watt (1975) among others to the Cromwell Joint Planning Committee and the Cromwell Borough Council. It was unprecedented in New Zealand in that it was primarily set up as reserve for the conservation of one species of small insect, the endangered chafer beetle *Prodontria lewisi*. The 81.4 hectare reserve is 1.5 kilometres south-west of the small town of Cromwell in Central Otago (fig. 1.1) and situated on the same river terrace. Over much of the reserve are small stabilised sand dunes, a once locally common post-glacial environment (Rance, 1990). Where dunes are absent, the substrate is a shallow, compact, gravelly loam (Watt, 1979).

Depletion of the natural vegetation of the reserve by rabbits continues to be a serious problem, though control measures are being undertaken. Management is being directed at increasing vegetation by planting native tussocks and reducing rabbit numbers. This is likely to be to the advantage of most native invertebrate species in the reserve, including the wētā (McKinlay and Gibson, 1993).

Potential predators of the Cromwell chafer beetle (and probably the wētā) include the introduced little owl (*Athene noctua*), hedgehogs (*Erinaceus europaeus*), feral cats (*Felis catus*), and rodents (*Mus musculus* and *Rattus* spp.) (Watt, 1979). Native skinks (*Leiolopisma* sp.) are present, but being diurnal (Watt, 1979), are unlikely to prey on either of these two nocturnal insects.

Invasive woody weeds such as *Pinus radiata*, broom (*Cytisus scoparius*) and sweet brier (*Rosa rubiginosa*), which potentially "choke out" all other vegetation, have been removed from the reserve (Armstrong, 1990).

Before the establishment of the area's protected status, there were two major vegetation communities present on the reserve: tussock grassland and tussock - scabweed associations (Watt, 1979). The former was an almost complete cover of silver tussock (*Poa cita*), sheep's sorrel (*Rumex acetosella*), *Hieracium* spp., St, John's wort (*Hypericum perforatum*), viper's bugloss (*Echium vulgare*), native willowherbs (*Epilobium* spp.) and pasture grasses, but lacked scabweeds (*Raoulia* spp.). The latter was a 40% - 100% cover dominated by *Raoulia* spp., *Echium vulgare*, *Hypericum perforatum*, *Hieracium* spp., *Epilobium* spp. and fescue grasses (*Festuca* spp.), but with less silver tussock.

Between 1986 and 1989, however, it was apparent that the vegetation cover in the reserve had deteriorated, probably caused by increasing rabbit numbers (Armstrong, 1990). A vegetation survey of three sections of the reserve in 1990 confirmed that silver tussock (*Poa cita*) was now rare and that adventive weeds such as *Rumex acetosella, Anthoxanthum odoratum* and *Echium vulgare* were dominant. Some other problem weeds were establishing or returning, such as wild thyme (*Thymus vulgaris*), *Pinus radiata*, broom (*Cytisus scoparius*), sweet brier (*Rosa rubiginosa*) and *Hieracium* spp. (Rance, 1990). Wild thyme in particular has become a characteristic weed of the Alexandra area (Emerson, 1994).

Revegetation of the reserve with silver tussock (*Poa cita*) of local genetic stock has been part of the reserve management strategy since 1986, and Rance (1990) recommended that this continues. Additionally it was suggested that other locally depleted or extinct native plant species (e.g. *Muehlenbeckia axillaris*) were re-introduced. A survey of plant recovery after rabbit poisoning was also recommended.

Assessing the risk of extinction for a species.

Before conservation action is taken for any species, the likelihood of further depletion must be assessed. To this end, the Department of Conservation, with assistance from the Department of Scientific and Industrial Research, Forest and Bird and other institutions has developed a set of criteria from which to assess the level of threat for any species (Tisdall, 1994). From this the relative priority for conservation action can be judged. The criteria assess five different factors which combine, with different weightings, to give an overall ranking. The factors are:

1. taxonomic distinctiveness,
2. status of the species,
3. threats facing the species,
4. vulnerability of the species,
5. human values.

The Cromwell *Hemiandrus* sp. is one of 37 currently known species of the genus, seven of which are considered threatened, so does not score highly on taxonomic distinctiveness. It is not considered specifically important by either most Māori or Pakeha people in New Zealand, so does not score highly on human values either. However, consideration of the other factors led to the taxon being classed as *category I* (species about which little information exists, but which are considered threatened) (Tisdall, 1994). The status of the species is precarious because there are very few known populations, the largest surviving on a small isolated area. The species is endemic to New Zealand and its limited range and considerable habitat specificity make it vulnerable. Threats facing the Cromwell *Hemiandrus* sp. include ongoing degradation or development of all non-protected habitats and possibly significant predation of the animals by introduced mammals and birds. Although invertebrates in general are relatively fast at breeding and therefore their populations can recover

quickly under good conditions (Rasch, 1992), such conditions may not be present for the Cromwell *Hemiandrus* species. Without research directed at management and the implementation of a management strategy, the species' conservation status is unlikely to improve.

Wētā conservation.

It is clear that most conservation efforts for New Zealand's threatened wildlife have concentrated on large animals with obvious public appeal, such as birds and sea mammals. However recently there has been a growing public awareness of (and scientific interest in) the conservation problems of New Zealand's invertebrate fauna. This may be due in part to the successful implementation of earlier conservation projects for endangered invertebrates (e.g. Meads and Moller (1978), working with the Cook Strait giant wētā *Deinacrida rugosa*), coupled with exciting and well publicised discoveries of relatively high visibility insect populations and species (e.g. giant wētā at Mahoenui, Mt. Somers and the Paparoa Ranges (Gibbs, 1994)).

The recent surge in interest in the conservation status of New Zealand wētā has been restricted largely to giant wētā (*Deinacrida* spp.) or other large species (the Mercury Island tusked wētā). The only exceptions are a major project on the Banks Peninsula tree wētā (Townsend, 1995) and some recent work on the small tusked wētā[5] from Northland (Gibbs, 1994). Since 1980, legal protection (via amendments to the Wildlife Act 1953) has been given to all the described species of *Deinacrida* except *D. connectens*, as well as the Banks Peninsula tree wētā *Hemideina ricta* (Gibbs, 1994).

Although less than 0.1% of New Zealand's invertebrate taxa are identified as threatened (Tisdall, 1994), the total number of taxa is large. Invertebrates comprise about 46% of all animal taxa identified as category A (highest priority threatened species), 42% of category B (second priority threatened species) and 31% of category C (third priority threatened species) (Tisdall, 1994).

In 1994, of the approximately 115 known wētā species (60 of which are rhaphidophorids) (Gibbs, 1994), 23 were recognised as threatened to some degree. These 23 comprised nine giant wētā (*Deinacrida* spp.), three cave wētā (three genera), two tusked wētā (two genera), one tree wētā (*H. ricta*) and eight ground wētā[6] (seven *Hemiandrus* spp., one not specified) (Tisdall, 1994).

The first species specific invertebrate conservation project in New Zealand was that by Meads and Moller (1978). The Cook Strait giant wētā (*D. rugosa*) used to occur on the mainland (Salmon, 1950), but by 1977 was confined to two or three rat-free islands in Cook Strait. Mana Island, which

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[5]The Northland tusked wētā is known as *Hemiandrus monstrosus* though this classification is not correct (Field, 1993).

[6]Note that in 1992 only one species of ground wētā (the Cromwell *Hemiandrus* sp.) was listed as threatened (Molloy and Davis, 1992).

was free of any significant wētā predators, held the only large population, while Stephens Island and Middle Trio Island had lower numbers, probably due to predation by their large populations of tuatara (Meads and Moller, 1978). Concern about the possible accidental introduction of rats to Mana Island in the 1970s led to the 1977 transfer of 43 juvenile and adult *Deinacrida rugosa* to Maud Island in Pelorus Sound (Marlborough Sounds). Like Mana Island, Maud Island lacks significant predators of giant wētā (Meads and Notman, 1992a). Several subsequent surveys of wētā distribution revealed that after a slow start, the population had expanded significantly (Meads, 1988). Ten years later it had spread about one kilometre in two directions from the release site (Meads and Notman, 1992a).

Since this successful relocation effort, populations of several other giant wētā species have been surveyed to estimate abundance and conservation status. Meads and Ballance (1990) briefly surveyed the only remaining population of the largest giant wētā, *D. heteracantha.* Before the introduction of predatory mammals such as ship rats (*Rattus rattus*) the species was widespread and common in the forests of Northland (Watt, 1963). By the turn of the century it was probably extinct on the mainland, surviving only on Great Barrier and Little Barrier Islands (Watt, 1963), and today exists only on the latter (Richards, 1973). The island is free of all introduced mammalian predators except kiore (*R. exulans*). However, the survey indicated that either the numbers were low enough to be of concern, or the wētā were more difficult to find than previous (anecdotal) observations would suggest. Despite the possibly significant decline in numbers of *D. heteracantha,* as yet nothing has been done apart from some captive breeding (P. Barrett, pers. comm.) to enhance its likelihood of survival.

A survey in 1992 (Meads and Notman, 1992b) covered areas in the Kaikoura ranges, South Island, where three species of *Deinacrida* are allopatric. *Deinacrida parva,* which is genetically very similar but morphologically and behaviourally distinct from *D. rugosa* (Rasch, 1992), was abundant above the bush line. Earlier searches in 1988 and 1989 revealed large numbers living in the forest and scrub in and around the upper Kowhai and Hapuku Rivers (Meads, 1989a). The second species, an as yet undescribed species of *Deinacrida* (at first known only from a sunbleached carcass found in 1953, but rediscovered in 1988), was found to be widespread but uncommon over the areas searched, but possibly exists in other suitable mountain bluff habitats. Indeed it seems that the Mt. Somers giant wētā, dramatically rediscovered in January 1994 after being known from only one specimen collected in 1957 (Gibbs, 1994), is the same species. The third species considered in the survey was the giant scree wētā (*D. connectens*), a relatively common alpine species known from many ranges of the Southern Alps.

The Mahoenui giant wētā (*Deinacrida* "mahoenui") has attracted much attention in recent years. Initially thought to be *D. heteracantha* (Watt, 1963), this similar but smaller species was discovered in 1962 and is the only known giant wētā surviving on the North Island mainland. Previous to 1980, several surveys failed to find more than one or two individuals, and concern for the species'

continued survival was great (Meads, 1987). About this time it was learned that the wētā inhabited areas of old gorse rather than the severely degraded tawa (*Beilschmiedia tawa*) forest remnants in the area. In 1990 the Department of Conservation purchased 240 hectares of this gorse as a Mahoenui wētā reserve, and densities in it are thought to be higher than those of any other giant wētā species (G. Sherley, pers. comm.). Conservation concerns have led to the wētā population in the reserve being subjected to intensive study. Sherley and Hayes (1993), investigated its demography, habitat use and distribution. Additionally, two new mainland populations have been successfully established nearby, and in 1993, 300 wētā were released onto Mahurangi Island (off the east coast of the North Island near Whitianga), as the nucleus of a new population (Gibbs, 1994). To date, these and the transfer of *Deinacrida rugosa* to Maud Island have been the only wētā translocations attempted.

One of the most striking insect finds this century was the 1970 discovery of the Mercury Island tusked wētā (undescribed), a very large ground burrowing species confined to one 10 hectare predator free island (Meads, 1990). This species, along with the population of *D. rugosa* on Mana Island, have been the subjects of radio tracking studies to help increase knowledge of their nocturnal movements.

A small giant wētā, *D. carinata*, is known from Herekopare Island (a predator free island in Foveaux Strait) (Rasch, 1992), and possibly other small islands. This species has the smallest range of all giant wētā, and being the only one for which no survey work has ever been attempted, its conservation status remains unknown (Rasch, 1992). However it seems likely that its numbers are now greater than before 1970. Feral cats had been present on the island since the 1920s, and a study in 1970, the year that the cats were eradicated, showed that some of them were eating very large numbers of wētā (Fitzgerald and Veitch, 1985). This indicates that the wētā were surviving considerable cat predation.

The North-West Nelson giant wētā (*D. tibiospina*) is a small, little known species. Described in 1950, only two specimens were ever collected until its "rediscovery" in 1984. A formal survey (Meads, 1989b) indicated that this wētā occurs in low densities over large areas of North-West Nelson above 1350m and is not threatened by habitat loss or predators.

A large scale survey has recently been completed for the Banks Peninsula tree wētā Hemideina ricta (Townsend, 1995). Once considered critically endangered (Rasch, 1992), this species is now known to be common on Banks Peninsula east of Akaroa Harbour (Townsend, 1995).

There are other giant wētā species for which no survey work has been undertaken as either they are not considered threatened (*D. fallai* from the Poor Knights Islands and the "Mount Cook" giant wētā from several localities in the Southern Alps) (Rasch, 1992) or have been recently discovered (the "Paparoa" burrowing giant wētā) (Gibbs, 1994).

Aims of the project.

The major research aims of the present work are as follows:

1. To investigate the life history (morphological development from egg to adult and the rate of growth of the instars over the seasons) of the Tekapo *Hemiandrus* species.

2. To investigate the distribution of the population within its habitat.

3. To investigate feeding ecology, parasitism of the wētā, and predation of the wētā by introduced mammals.

4. To collect all known records and observations of the Cromwell species and gauge its similarity to the Tekapo species.

5. To interpret any relevant findings on the Tekapo River *Hemiandrus* sp. in the formulation of recommendations for a programme to enhance populations of the Cromwell species (and perhaps other threatened species of *Hemiandrus*).

Chapter 2
Study Area

Field work for the present study was undertaken on stabilised outwash terraces of the lower Tekapo River, in the Mackenzie Basin, South Canterbury.

History of the area.

In pre-European times, human use of the Mackenzie Basin (fig. 2.1) was limited to intermittent hunting expeditions by Māori (O'Connor, 1976). By the late 1850s, pastoralism had become important, and by the 1870s had expanded to cover most of the basin, with primarily merino sheep being raised for their wool (Waitaki Catchment Commission, 1982). In the past three decades rabbit control programmes, topdressing and oversowing have allowed intensification of pastoral farming in some areas (O'Connor, 1976).

Since the commissioning of the Waitaki Dam in 1935, the upper Waitaki catchment has seen a huge investment in hydroelectric power generation. Presently the waters of all the catchment's major rivers except the Ahuriri River are used for this purpose (Waitaki Catchment Commission, 1982). Ongoing development has over the decades caused the flooding of 40 km of braided river, 150 km^2 of terraces, flats, swamps, streams and ponds, and has de-watered about 85 km of the beds of the Ohau, Tekapo and Pukaki Rivers (A. Warren, pers. comm.).

In 1990 Electricorp New Zealand (E.C.N.Z.) applied to the Canterbury Regional Council for a renewal of its right to use the water resources of the Waitaki catchment (E.C.N.Z., 1990). However for many years the Wildlife Service and later the Department of Conservation (D.o.C.) had recognised that the braided rivers of the Waitaki catchment were of great significance for conservation, as habitats for many increasingly rare endemic species, especially birds. In a pioneering agreement between conservation and development interests, D.o.C. and E.C.N.Z. developed Project River Recovery (P.R.R.), whereby D.o.C. would provide the expertise for a long term wetland restoration project, and E.C.N.Z. the money. Funding is a condition of the 35 year water right and is guaranteed until at least the end of it (Department of Conservation, 1993).

The principal aim of P.R.R. is to provide greater areas of habitat for threatened endemic bird species, some of which are confined to the braided rivers of the Waitaki catchment. Populations of some of these birds have declined considerably due to predation, loss of habitat from flooding or de-watering of feeding and nesting areas and degradation of these areas by the invasion of weeds (Department of Conservation, 1993).

The invasion by weeds of de-watered riverbeds and much surrounding land in the Mackenzie Basin is

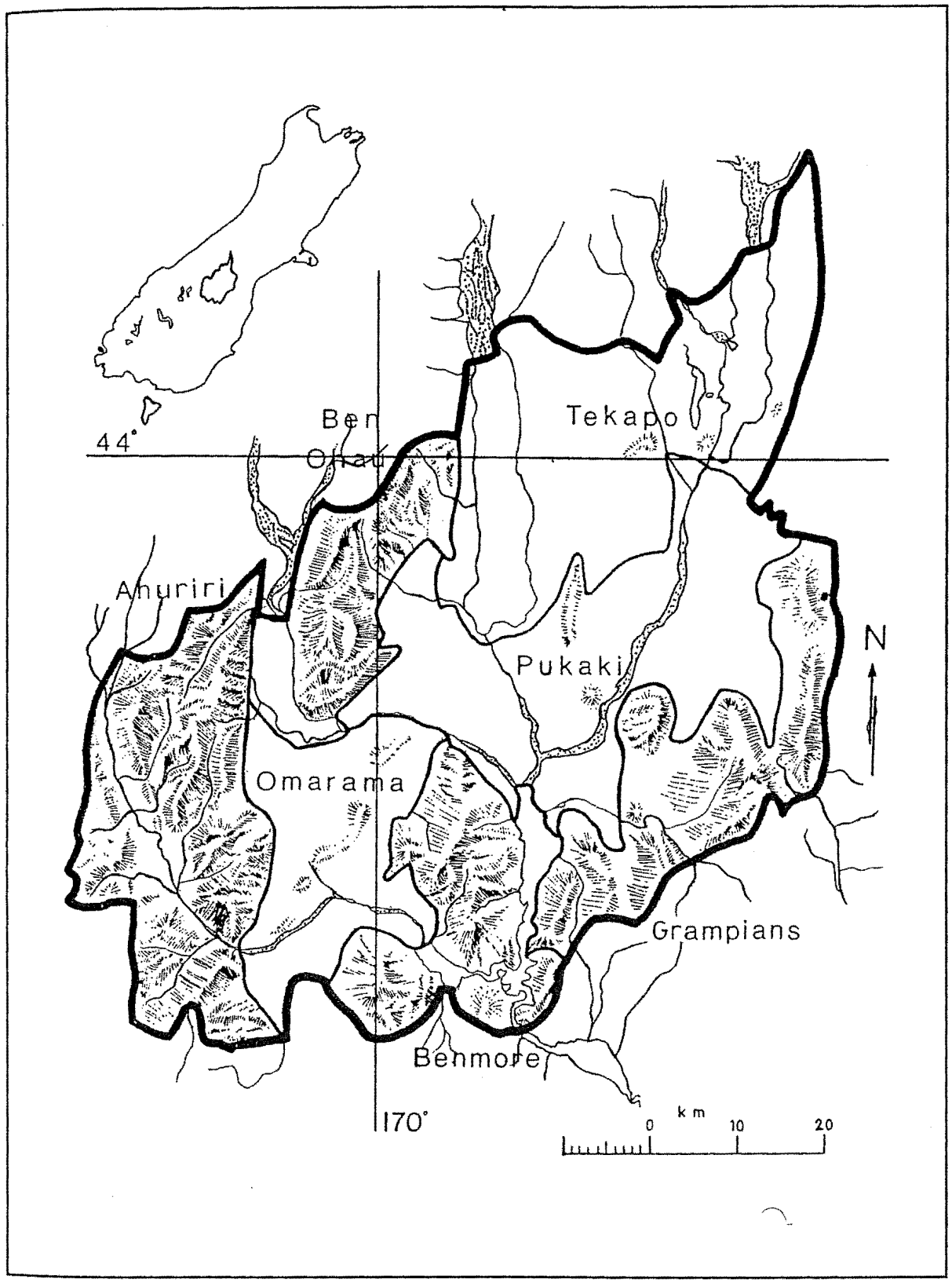

Figure 2.1. Map of the Mackenzie Ecological Region (heavy border) and its constituent ecological districts. The Mackenzie Basin includes most of the flat land of the Tekapo and Pukaki Ecological Districts (from Espie et al., 1984).

likely to have had an effect on other fauna also. Several species of grasshopper (Orthoptera: Acrididae) occur in the area, including two which are localised and rare (*Sigaus minutus* and *Brachaspis robustus*). The latter is New Zealand's most endangered endemic grasshopper (Bell, 1986). Although it has not been studied (since past populations are unknown) it is likely that these and many other species' habitat would be less suitable now than before the advent of weeds, grazing and fires.

Geology.

The Mackenzie Basin is a large flat to undulating plain surrounded by block mountains to the south, east and west, and glaciated alpine areas to the north (O'Connor, 1976). A thick layer of Pleistocene fluvioglacial outwash gravels covers most of the basin with the exception of isolated hills formed from resistant basement greywacke. These gravels cover tertiary sediments which overlie the deep bedrock (Espie et al., 1984).

The present study site is situated on alluvial gravels and recent soils on floodplains and low outwash terraces adjacent to the Tekapo River. Since 1977 the majority of water from the Tekapo catchment has been diverted via a canal to Lake Pukaki for hydroelectric generation, so only the very lowest terraces adjacent to existing channels have flooded (Waitaki Catchment Commission, 1982).

Climate.

The climate of the Mackenzie Basin is described as sub-continental. It is characterised by warm summers and cold winters, and the basin is the driest part of the Mackenzie Ecological Region (fig. 2.1). Ranges to the north and west receive frequent heavy rains and high annual precipitation (typically 2500mm - 3200mm), but heavy sustained falls are rare in the basin (Espie et al., 1984).

Much of the Pukaki Ecological District (fig. 2.1) is semi arid and receives about 550mm - 600mm precipitation per annum. The present study was conducted in the driest part of the Mackenzie Basin, close to the 600mm isohyet (Waitaki Catchment Commission, 1982).

Predominant winds are warm föhn winds from the north-west, which when very strong (usually in summer) can cause loss of soil in areas of depleted vegetation. Low rainfall coupled with free draining soils and warm winds lead to frequent droughts and very low humidity at all times of the year (Waitaki Catchment Commission, 1982).

Vegetation: historical and present.

Evidence suggests that before human presence, vegetation in the Mackenzie Basin was dominated by dry conifer and broadleaf forest, except perhaps on regularly flooded river terraces (McGlone, 1989).

Subfossil matai (*Podocarpus spicatus*) seeds have been found in terraces near Lake Tekapo, and podocarp charcoal is present in several sites in and near the basin (Molloy et al., 1963).

Early Māori fires removed all forest from the basin and most of the surrounding hills, and since then tussock grasslands have been the dominant vegetation communities (Espie et al., 1984). Forest never re-established, possibly due to a climatic change to lower temperatures and rainfall (Espie et al., 1984). By the time of European settlement the basin's dry plains were dominated by fescue tussock and scrub communities (McGlone, 1989).

When pastoralists first introduced sheep into the Mackenzie basin in 1857, they began the practice of burning to encourage palatable new growth in the existing grasses (Connor, 1964). While repeated burning did produce valuable new feed for the heavy stock loads, in some areas the effects have been disastrous. Large tracts of depleted vegetation, weed associations, bare land and erosion have resulted (Connor, 1964). Additionally, overgrazing by stock and large numbers of rabbits, coupled with periods of financial stress for farmers (e.g. in the Depression of 1929 - 1934), have contributed to several major episodes of degradation (O'Connor, 1976).

The present study was on recent river terraces with severely depleted grass and scrub communities (fig. 2.2). The most abundant native plant species apart from lichens included a low creeping vine (*Muehlenbeckia axillaris*), scabweed (*Raoulia australis*), willowherbs (*Epilobium* spp.) and matagouri (*Discaria toumatou*), all of which are colonisers of disturbed ground. Adventive weeds were abundant and dominated by sweet brier (*Rosa rubiginosa*), viper's bugloss (*Echium vulgare*), stonecrop (*Sedum acre*), woolly mullein (*Verbascum thapsus*), hawkweeds (*Hieracium* spp.) and sheep's sorrel (*Rumex acetosella*). Much bare ground, stones, shingle and sand were present.

In some areas, especially close to the Tekapo delta, extensive areas of exotic conifers have been planted and are wilding. Two species were present; Scots pine (*Pinus sylvestris*) and Ponderosa pine (*P. ponderosa*). The trees were planted by the Ministry of Works in 1981 and 1982 on what were then considered the best silty soils in the area (N. Buttery, pers. comm.).

Comparison of the study area with the Cromwell site.

From the above it is apparent that the known habitat of the Cromwell wētā and the present study site are similar in floral composition. Large populations of rabbits are present in and around each site, compounding problems of depleted vegetation, exposed soils and wind erosion (Waitaki Catchment Commission, 1982). Dust storms are a common occurrence in inland South Canterbury during strong dry winds (Kirk, 1990), and the study area is classified as a region of moderately severe wind erosion (Waitaki Catchment Commission, 1982).

The Tekapo and Cromwell wētā both burrow in recent shallow soils overlying stable alluvial river

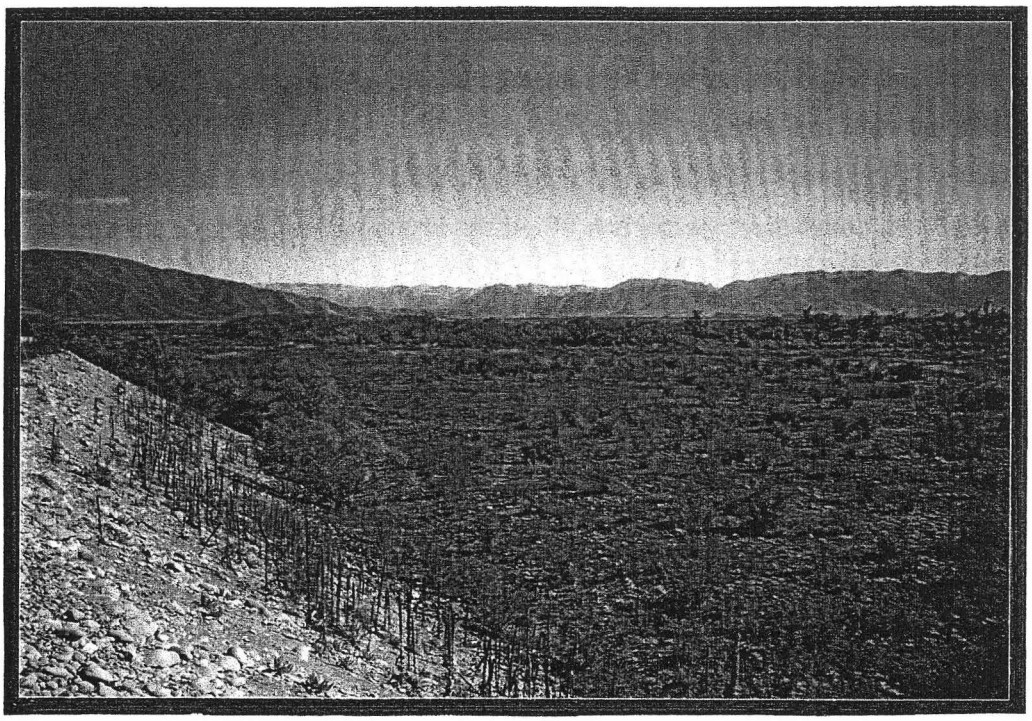

Figure 2.2. Typical *Hemiandrus* new sp. habitat on terraces of the Tekapo River: note willow trees (*Salix* spp.) in the background near the river (April 1994).

terraces. Both regions experience low rainfall, very high evaporation rates, hot dry summers with high sunshine hours and cold winters with frequent severe frosts (New Zealand Meterological Service, 1983). Table 2.1 summarises several climatological parameters of the present study site and the Cromwell site. Climatic conditions at Twizel, (460m altitude and 15km from the study area), are assumed to be representative of those at the study area (about 400m). Values for Alexandra are included because the Cromwell *Hemiandrus* species is also known from there.

Table 2.1. Altitude and climatic data for Twizel, Cromwell and Alexandra; means of all recorded years up to 1980 (from New Zealand Meterological Service, 1983).
Note: values are rounded to the nearest whole number.

	Twizel	Cromwell	Alexandra
Altitude (m)	460	213	141
January mean daily high (^{0}C)	23	24	23
January mean daily low (^{0}C)	9	11	11
July mean daily high (^{0}C)	6	8	7
July mean daily low (^{0}C)	-3	-2	-2
mean annual rainfall (mm)	646	401	343
mean annual sunshine (hrs.)	2120	not available	2064
mean annual days frost	175	174	154

Introduced predatory species which may affect the populations of wētā in both areas are feral cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), little owls (*Athene noctua*), rats (*Rattus* spp.), mice (*Mus musculus*) and possibly mustelids (e.g. *Mustela furo*). All these species, especially hedgehogs, rats and little owls, are known to eat insects when available (Dept. of Lands and Survey, 1984) and being nocturnal, are likely to encounter wētā.

Chapter 3
Distribution and Habitat Use

Introduction.

The Tekapo ground wētā (*Hemiandrus* new sp.) was first found in a few sites adjacent to the Tekapo River delta in December 1992 (Sinclair, 1995). Small scale pitfall trapping of this area and others indicated that the species was distributed throughout the river terraces, but in much higher densities in some places than others. For example, in an invertebrate sampling study of the same general area, wētā were not usually trapped in wet areas, sites with grass and willow trees (*Salix* spp.) or recently disturbed areas (L. Sinclair, pers. comm.). In addition to the sites covered by the present study, specimens were trapped on a high terrace to the west of the delta, as well as in open areas along the northern banks of the lower reaches of the Tekapo River.

The aim of this section of the study was to investigate the distribution of *Hemiandrus* new sp. relative to habitat variables such as substrate type and depth, and plant abundance. Additionally, two hypotheses were experimentally tested. The first hypothesis was that the relative abundance of wētā in an area planted in pine trees (*Pinus* spp.) was the same as that in adjacent non-planted areas. This was of interest for two reasons. Firstly there is evidence that most of lowland South Canterbury and Central Otago (including the current habitats of both the Tekapo and Cromwell wētā) was forested in pre-human times (McGlone, 1989) (see chapter 2), so both species may have evolved in forest habitats. It is therefore possible that the present distribution of wētā is influenced by the "return" of forest. Secondly it is believed that the proliferation of plantation forestry in the Cromwell area is the greatest threat to the continued existence of the Cromwell *Hemiandrus* species (McKinlay and Gibson, 1993).

The second hypothesis tested was that wētā abundance does not change with increasing distance from the riverbed. If this hypothesis proved false, that would mean that the species' distribution is somehow dependent on proximity to the river.

Methods.

1. Distribution relative to habitat variables.

Preliminary investigative sampling in September 1993 indicated that open sandy or silty areas of river terrace were likely wētā habitat. Four sites along the south east banks of the Tekapo River were chosen for sampling (fig. 3.1). The sites were each large, continuous and flat, generally lacking willow trees, recent river channels or extensive wet areas (all considered unlikely wētā habitat). All sites were easily accessible and were higher than present likely flood levels.

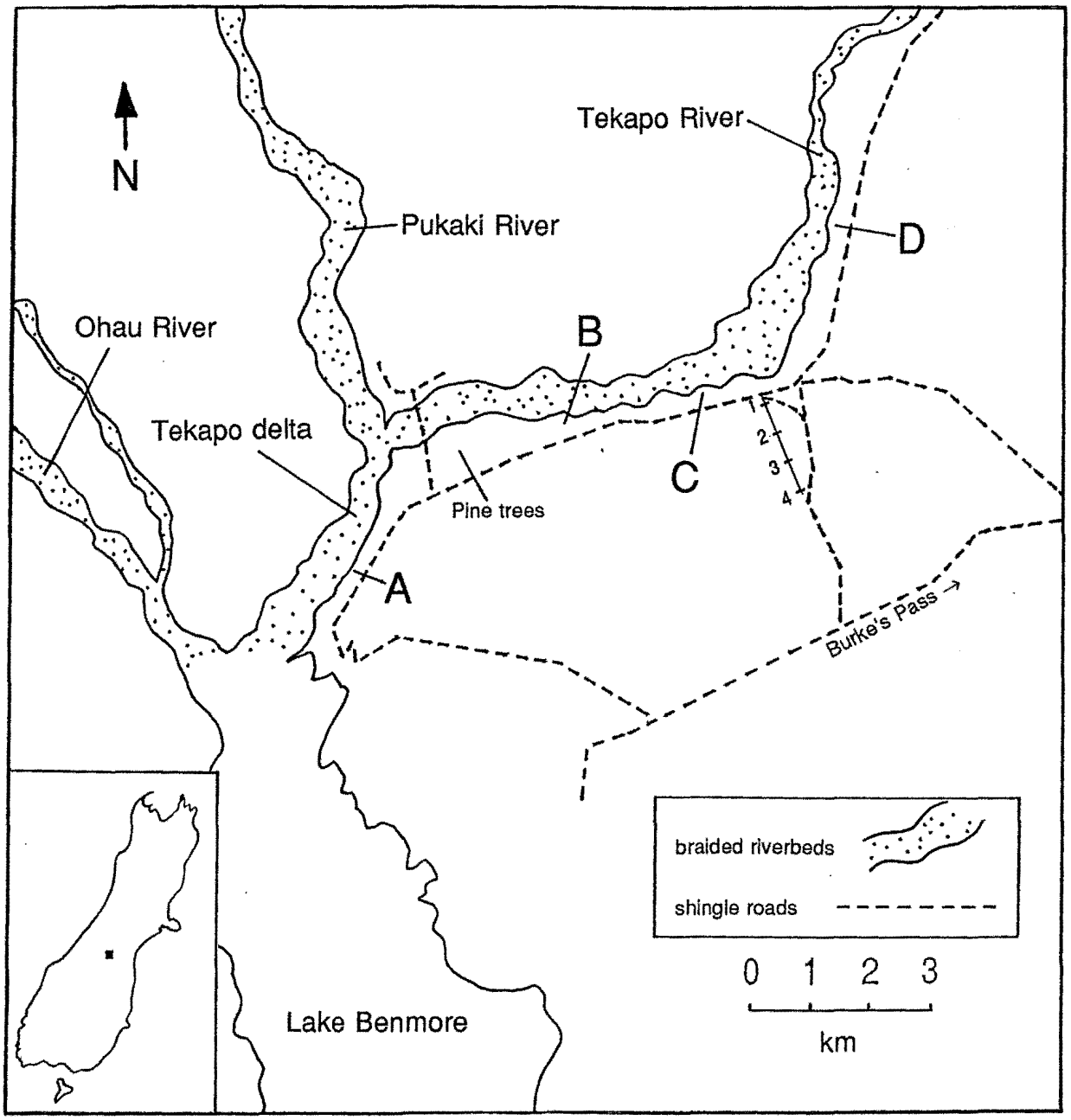

Figure 3.1. Map of the study area, indicating sampling sites (A, B, C, D) and other locations referred to in the text.

Lines of five pitfall traps were placed at intervals of about 100 metres at each site. Each line was laid perpendicular to the river's flow, and where possible, the five traps were spaced evenly between the road and the nearest river channel. No trap was positioned less than about seven metres from any other. Site A was the largest site, with seven lines of five pitfall traps extending alongside the Tekapo delta. Sites B, C and D were 2.5, 5 and 9 kilometres respectively upstream of the delta and each consisted of two lines of five traps (fig. 3.1).

Sampling began in October 1993 and continued until January 1995. Only one sample was made during the coldest months (from May to August 1994)[7] (table 3.1).

Table 3.1. Dates of monthly sampling and trap sites used.

month	dates of trap nights	date of new moon	trap sites used
Sep. 1993	19th, 20th	16th	preliminary
Oct. 1993	20th, 21st, 22nd	16th	A
Nov. 1993	13th, 14th, 15th	14th	A
Dec. 1993	12th, 13th, 14th	13th	A
Jan. 1994	12th, 13th, 14th	12th	A B C D
Feb. 1994	9th, 10th, 11th	11th	A B C D
Mar. 1994	11th, 12th, 13th	12th	A B C D
Apr. 1994	12th, 13th, 14th	11th	A B C D
May 1994	no sample	11th	-
Jun. 1994	28th, 29th, 30th	9th	A B C D
Jul. 1994	no sample	9th	-
Aug. 1994	no sample	7th	-
Sep. 1994	6th (rain shortened)	6th	A B C D
Oct. 1994	4th, 5th, 6th	5th	B C D
Nov. 1994	2nd, 3rd, 4th	4th	B C D
Dec. 1994	4th, 5th, 6th	3rd	B C D
Jan. 1995	3rd, 4th, 5th	1st	B C D

From October 1993 until December 1993 inclusive, only site A was in use. In January 1994, sites B, C and D were opened and these operated until January 1995 inclusive (table 3.1). As the time

[7]Wētā activity during the cold months may have been so low that few if any wētā would have been trapped (see chapter 4).

required each morning to check all the live traps was too great with all sites operating, and other work had to take priority, it was decided to discontinue the use of site A after September 1994. The September 1994 sample was shortened to one trap night after sustained heavy rain flooded the traps.

Pitfall traps were the only apparatus used to sample wētā (see appendix 1 for a discussion of the problems and advantages of using pitfall traps). Two types of pitfalls were used. Initially, all traps were standard "kill" pitfalls; plastic pottles with a diameter of 110mm and a depth of 120mm. To each "kill" trap, 200 ml of a mixture of one part ethylene glycol to two parts water was added. Ethylene glycol, when used as a preservative and killing agent, has the advantages of being odourless to invertebrates (Duffey, 1962) and safe to humans if used carefully. It appears to be the most popular preservative used in recent pitfall studies (e.g. Luff and Eyre, 1988; Topping and Sunderland, 1992). An alternative, formaldehyde, can attract insects (Luff, 1968), as may alcohol (Greenslade and Greenslade, 1971). Ethylene glycol has the added advantage of not evaporating over periods of a few days or weeks. Some workers have added a small amount of detergent to the preservative as a wetting agent (e.g. Kempson et al., 1963; Topping and Sunderland, 1992). From laboratory observations, however, it was noted that once a specimen of *Hemiandrus* new sp. fell into a pitfall, it could not escape and its struggles caused it to wet quickly. To eliminate the risk of making the preservative solution detectable to wētā, detergent was not added.

The traps were dug into the substrate with the rim made flush with the surface. Care was taken to avoid undue disturbance of surrounding ground as that may have affected the likelihood of wētā approaching the traps (Greenslade, 1973).

The second type of pitfall trap caught wētā alive. These "live" traps replaced about half of the original "kill" traps. "Live" pitfalls were made from two litre plastic soft-drink bottles. Each bottle was cut transversely about 150mm from the bottom. The top section was then trimmed, inverted, and placed into the bottom section to form a funnel (fig. 3.2). This funnel prevented escape of wētā and could easily be removed when the trap was checked. These traps had the same diameter as the "kill" pitfalls and were dug into the substrate in the same way. No preservative solution was added and any captured live wētā could be found amongst the convolutions in the bottom of the bottle. These "live" traps were far simpler and more convenient to use than any others tried, (such as those incorporating metal funnels), and were cheaper to make in large numbers.

"Kill" and "live" pitfall traps captured wētā with similar efficiency (see appendix 2 for an experiment investigating the relative trapping efficiencies of the two trap types).

In the field, pitfalls were set for three consecutive nights during each visit. All traps were checked each morning. Wētā found in the "kill" traps were removed and washed in water, before being labelled and preserved individually in 70% ethanol. Wētā from "live" pitfalls were housed individually in labelled one litre plastic pottles, with moist soil added. In hot weather "live" traps

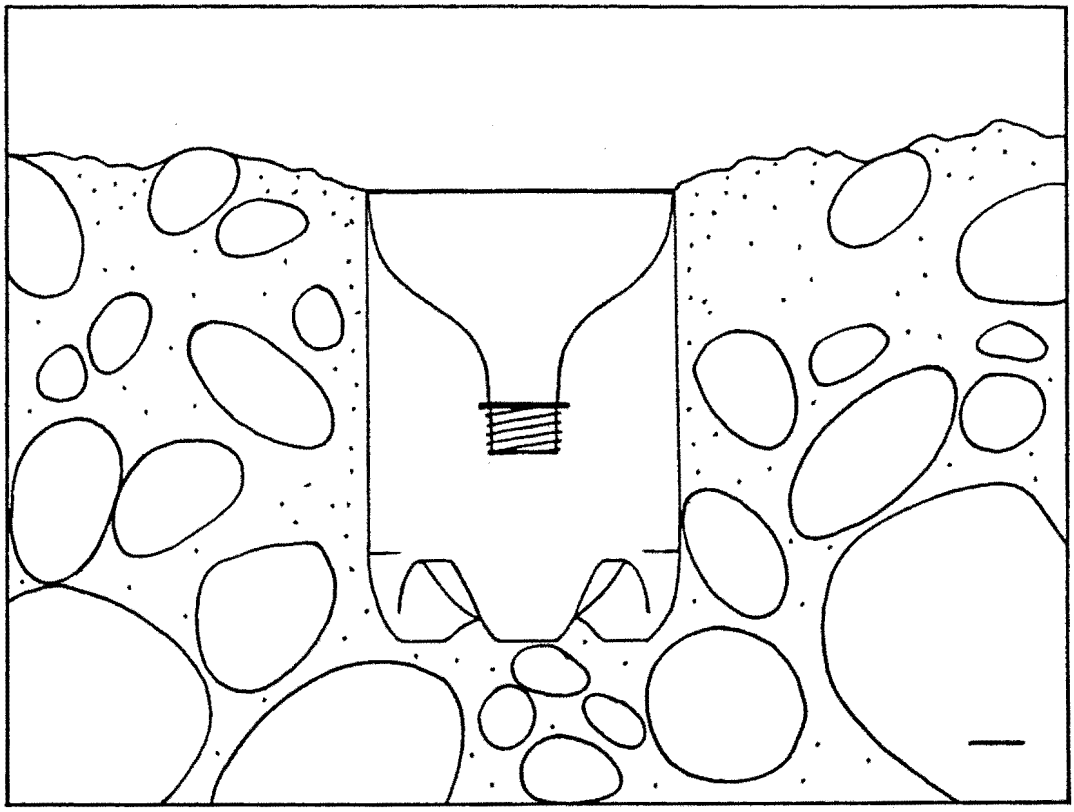

Figure 3.2. Diagram showing the construction of a simple "live" pitfall trap. The top of a 2*l* plastic soft-drink bottle is cut off and inverted in the lower section, forming a funnel to prevent escape of trapped animals. Scale bar = 20mm.

were emptied as early as possible to avoid the risk of captured animals overheating or desiccating.

Samples were conducted approximately monthly, as near as practical to the new moon (table 3.1). The purpose of this schedule was to maximise catches as it has long been known that insect activity is greatest on the darkest nights (see appendix 3 for a discussion of the effects of moonlight on insect activity).

All traps were left closed *in-situ* between the monthly sampling periods to avoid additional disturbance of the surrounding substrate.

The cumulative catch for each trap in sites B, C and D for January 1994 to January 1995 inclusive (28 trap nights) was recorded. As the frequency distribution of wētā catch was highly skewed to the left, wētā data were normalized with a log transformation.

Characteristics of each plot were recorded during December 1994 and January 1995. A quadrat (4m x 4m) was placed around each trap (with one side oriented north-south) and an estimate of the abundance of each plant species present scored. The scoring took account of both the abundance of the species present the size of the plants. The scoring was subjective but consistent between the two scorers and between repeats of the same quadrat. Plant abundance was ranked as follows:

0 = absent
1 = rare
2 = occasional
3 = frequent
4 = abundant
5 = dominant.

Plant species were classified as one of the following functional groups: ground cover (e.g. *Raoulia australis*), intermediate (e.g. most grasses) or shrub layer (e.g. *Rosa rubiginosa*), and as either native or adventive. The five species of lichens commonly recorded were classed in their own group (see appendix 4 for the species list and classifications). Abundance scores for all species in each group were summed and the totals regressed against the total catch of wētā in each plot using a best subset multiple regression (Statistix 4.0) (K. Duncan, pers. comm.).

Bare ground (i.e. ground not covered in plants) dominated most quadrats and the substrate fell into three major classes. The percentage of each quadrat covered by these classes was estimated. The substrate classes did not conform exactly to classes in the standard Udden-Wentworth grain-size scale, but were approximately as follows: class 1 (< 1mm diameter) = *coarse sand* or finer; class 2 (1 - 4mm diameter) = *very coarse sand - granule*; class 3 (> 4mm diameter) = *pebble* or larger (Lewis, 1984).

The depth of "burrowable" substrate present in each quadrat was also scored. A 5mm thick metal rod with centimetre divisions inscribed on it was pushed into the substrate at five positions in each quadrat, and the depth to which it could penetrate recorded. The mean of these five values gave an estimate of the local depth of "burrowable" substrate available to burrowing species like wētā. This measurement was attempted only for areas of class 1 as the rod would not satisfactorily push into substrate with larger grain sizes and wētā probably can not burrow there (see chapter 6). For each plot the class 1 substrate area estimate was multiplied by the class 1 depth measurement to give a relative estimate of the amount of the substrate. This new substrate variable was added into the multiple regression model.

2. Wētā abundance in a plantation forest.

Between April 1994 and January 1995 an experiment was performed to investigate the relative abundance of wētā on an area of river terrace planted with pine trees (predominantly *Pinus sylvestris*, with some *P. ponderosa*). The trees were planted by the Ministry of Works in the early 1980s (N. Buttery, pers. comm.) and are about four to five metres tall. The abundance of wētā within this area of pine trees was compared to that of two areas lacking trees. Fourteen "kill" pitfalls were set within the plantation area, and seven were set in each of two nearby areas without trees, (one immediately to the east and one to the west). Unlike other traps, these pitfalls operated continuously, initially for 15 nights (15 April - 29 April 1994 inclusive), and later for 93 nights (5 October 1994 - 5 January 1995 inclusive). During the second sampling period the traps were checked and emptied at the beginning and end of each monthly field session[8]. Total numbers of wētā caught in each trap after the 108 nights were recorded.

3. Wētā abundance away from the riverbed.

A second sampling experiment was set up in November 1994. The aim was to compare wētā abundance, as indicated by "kill" pitfall captures, in plots of varying distances from the river bed. As the entire river is surrounded by pasture in this area, the plots were predominantly over grazed land. Four groups of eight pitfalls were set at increasing distances from the river, the first at approximately 200m, the second at 600m, the third at 1100m and the fourth at 1500m (fig. 3.1, numbers 1 - 4). Each trap was placed at least 10m from any other. The traps operated continuously from 6 October 1994 - 7 January 1995 inclusive (a total of 94 nights) and were cleared as for the previous experiment.

[8]Data from those wētā trapped during the three day field sessions were incorporated into data sets for chapter 4 (Life History and Development) as well as the present chapter. Other wētā trapped here could not be so used as their dates of capture were uncertain.

Results.

1. Distribution relative to habitat variables.

The best subset regression (Statistix 4.0) revealed that one variable (the substrate variable generated by multiplying class 1 substrate area by its mean depth) was by far the best individual predictor of wētā abundance ($r^2 = 0.41$). The best model incorporating two variables added the variable generated by summing the abundance scores for all lichens. This model explained over 50% of the variation in wētā abundance ($r^2 = 0.51$). The best three variable model added the variable "total large shrubs" generated by summing the abundance scores for the three species of large shrubs recorded (*Rosa rubiginosa, Discaria toumatou* and *Melicytus alpinus*). This model explained slightly more of the variance in wētā catch ($r^2 = 0.54$). Adding more variables to the model decreased the r^2 value from this point on. Additionally the C_p score was lowest for the best three variable model. C_p is a measure of "total squared error" for each fitting equation (Daniel and Wood, 1980). As it increases with a model's complexity but decreases with its predictive power, the lowest score indicates the best model (Daniel and Wood, 1980).

There appeared to be no relationships between wētā abundance and any of the following variables: total abundance of native plants, total abundance of adventive plants, total abundance of ground cover plants and total abundance of intermediate plants.

2. Wētā abundance in a plantation forest.

Nearly four times as many wētā were trapped in the "forest" area than the "non-forest" area. The mean number of wētā caught per trap, sample standard deviation (s) and total wētā caught for both areas are given in table 3.2. To test whether the means came from a population with equal μ, the *t*-test of significance for differences between means was employed (Sokal and Rohlf, 1981). The difference between the two means was significant at $\alpha < 0.001$ ($t_s = 6.72$; $t_{\text{critical [d.f.} = 26,\ \alpha = 0.001]} = 3.71$).

Table 3.2. Wētā capture data from "forest" and "non-forest" areas.

	forest (n = 14)	non-forest (n = 14)
$\bar{x}$ wētā caught	19.71	5.14
s	7.68	2.63
total wētā caught	276	72

3. Wētā abundance away from the riverbed.

Similar numbers of wētā were caught in each of the four areas at increasing distances from the riverbed. The mean number of wētā caught per trap, sample variance (s^2) and total wētā caught for each area are given in table 3.3.

Table 3.3. Wētā capture data from plots at increasing distances from the riverbed.

	distance from river			
	200m	600m	1100m	1500m
$\bar{x}$ wētā caught	8.67	12.50	9.33	11.33
s^2	27.07	26.70	11.87	23.46
total wētā caught	52	75	56	68

A single classification Model 1 Anova was performed on these data (Sokal and Rohlf, 1981). Firstly an F_{MAX} test of homogeneity of variances was performed to establish the validity of proceeding with the Anova. The calculated F_{MAX} of 2.28 was much less than the tabulated critical $F_{MAX\ [\alpha = 0.05;\ 4,5]}$ of 13.7, indicating that the variances were homogenous and the Anova should proceed.

The hypothesis of interest being tested was whether the groups of traps at increasing distances from the riverbed captured differing numbers of wētā. If so, this would indicate that the distribution of wētā is somehow associated with proximity to the riverbed. Table 3.4 presents the results of the calculations.

Table 3.4. Anova table for proximity to riverbed data.

Source of variation	*df*	*SS*	*MS*	F_s
between groups	3	56.46	18.82	0.845
within groups	20	445.50	22.28	
total	23	501.96		
$F_{0.05\ [3,20]} = 3.09$: $F_s << F_{0.05\ [3,20]}$ so accept the null hypothesis.				

The non-significant result of the Anova shows that the groups of traps did not capture significantly different numbers of wētā, indicating that wētā distribution is independent of proximity to the riverbed.

Discussion.

Of all the independent variables measured, the relative amount of fine silt substrate (grain size < 1mm) present in plots was the most important determinant of wētā abundance. This is likely to be because fine friable substrate is required for wētā burrowing. Indeed, burrows were only found in places where the substrate was predominantly silty (see chapter 6 on burrowing) indicating that wētā are most abundant in these places.

The summed abundance of lichens added a small amount of predictive power to the multiple regression model, as did the summed abundance of large shrubs (dominated by *Rosa rubiginosa*). Perhaps wētā utilize some lichen species as a food source so tend to be found in those areas where lichens are most abundant. Another hypothesis is that because some lichens (especially *Neofuscelia* sp., *Cladia aggregata* and *Chondropsis semiviridis*) grow mostly on rocks and ground devoid of vegetation, their habitats coincide to some extent with the non-vegetated silty places preferred by wētā. This may be especially true of *C. semiviridis*, a common, small unattached lichen which blows around and can accumulate in sheltered flat places. However, although the abundance of *Neofuscelia* sp. was highly correlated with the percentage of quadrat area covered by class 3 substrate (pebbles and larger rocks), the abundance of other lichen species did not correlate strongly with the percentage area of non-vegetated ground.

The reason that large shrubs (*Rosa rubiginosa, Discaria toumatou* and *Melicytus alpinus*) appear slightly more abundant in areas with more wētā may be ultimately linked to the plants' and the wētā's common preference for a substrate type rather than some dependence that the wētā have on the shrubs.

It is particularly interesting that wētā were significantly more abundant in the "forested" area than adjacent non-planted areas. Two possible explanations are suggested. The first is that *Hemiandrus* new sp. evolved from a forest-living ancestor similar to many other forest-living ground wētā today, and is better adapted to the conditions found under a forest canopy. A second explanation for the higher abundance in the planted area is that the then Ministry of Works, when planting the trees, selected an area with substrate suitable both for the growth of trees and for wētā (that is with relatively deep silty soil). This is apparently the case, as the Ministry of Works in the early 1980s selected tree species for their plantations to suit the local soil types (N. Buttery, pers. comm.). The presence of the trees does not seem detrimental to the wētā population.

Interestingly, McKinlay and Gibson (1993) stated that pine forestry was a significant factor in the loss of populations of the Cromwell *Hemiandrus* sp., as accumulating needles and prunings exclude other vegetation. Perhaps an even more significant threat would be from the considerable ground disturbance when the trees are finally harvested. It is worth noting that the diversity and abundance of other plant species in the planted area were very low, but fallen needles, although present, were not smothering other vegetation completely[9], and prunings were absent (personal observation). Additionally the trees were not particularly vigorous and did not form a continuous canopy in most places.

It appears that the distribution of the Tekapo wētā may extend a considerable distance from the riverbed across areas where suitable substrate is found and is not limited to the more recent terraces

[9]The native vine *Muehlenbeckia axillaris* in particular was thriving amongst fallen needles.

near the river. Much of the surrounding farmland is flat and composed of stony outwash terraces like the study site. It is unknown whether the distribution of *Hemiandrus* new sp. extends into the nearby hills surrounding the plains. The presence of large grazing animals (sheep and cattle) on the farms is unlikely to be much more significant to the distribution of wētā than the presence of high densities of rabbits in non-farmed areas. Rabbits disturb the ground directly by their burrowing and indirectly by destroying vegetation which binds the soil, both potentially increasing soil loss from wind erosion. A potential detrimental effect that the larger animals have on wētā habitat that rabbits may not is the compacting of soil by their hooves.

Other ground disturbance may have an effect on the distribution of *Hemiandrus* new sp. It was noted that the only pitfall traps which never caught any wētā during the course of the entire study were a few in a small group near the south end of the Tekapo delta, not far from Haldon camping ground. In general, wētā abundance appeared to increase with distance from this area (personal observation). It is possible that substrate disturbance caused by anglers' and shooters' vehicles as well as large numbers of recreational motorcycles and four-wheel drives during the summer decreases the suitability of the habitat for wētā close to the camping ground.

Chapter 4
Life History and Development

A. Life cycle.

Introduction.

This section traces the stages of growth and development of *Hemiandrus* new sp., as well as the development of cohorts over the seasons.

Few workers have investigated the life cycles of ground wētā. Wahid (1978), working on the only known pest wētā species (*Hemiandrus* "peninsularis" from Banks Peninsula and the Port Hills, Christchurch)[10] found seven to nine instars in males and eight in females. He considered that oviposition occurred in April, eclosion (hatching of eggs) in December, and that the life cycle took two years to complete. Adult females stayed with their eggs (which they laid in their burrows) for the quiescent (dormant) period over winter. The second quiescent winter period was endured by sixth and seventh instar individuals (Wahid, 1978).

The ground wētā *Zealandosandrus gracilis* had seven male and nine female instars (Cary, 1981). It was proposed that males may incur some advantage from developing earlier, in that they can mate with more females over a longer period. Females may benefit from the extra two developmental stages by having more time to meet extra nutrient requirements for ovarian development (Cary, 1981). It is normal for the larger of the sexes to have the higher number of instars (Chopard, 1938). Ramsay (1964) asserted that where the sexes differ in moult number, the female has the higher number in all groups of Orthoptera except the Rhaphidophoridae (cave wētā). However, many authors failed to distinguish between the sexes when recording moult number, so important exceptions may have escaped attention. Within the Gryllacridoidea (the superfamily including wētā), six to eleven instars are known, with six to nine being most frequent (Ramsay, 1964).

Seasonality has been investigated in a few wētā species. The eggs and most instars of *Z. gracilis* were recorded in every month of the year (Cary, 1981), indicating that its development is not synchronised with the seasons. Of giant wētā, the life cycle of *Deinacrida rugosa* (the Cook Strait giant wētā) was seasonal (Ramsay, 1955), while those of the more northern species *D. fallai* and *D. heteracantha* were not (Richards, 1973). Of cave wētā (Rhaphidophoridae), *Pachyrhamma fascifer* developed seasonally (Richards, 1953), as did *P. waitomoensis*, but a close relative *P. turneri* did not (Richards, 1961).

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[10]This species (*Hemiandrus* "peninsularis") is an occasional pest of orchards in Horotane Valley, Christchurch, and nearby fruit growing areas (Wahid, 1978).

It is a reasonable hypothesis that species inhabiting areas with the most seasonal climates would have the most seasonal life cycles (Cary, 1981). However, this is not always the case for those wētā species in which seasonality has been investigated. The life cycles of many insects may be more closely associated with the availability of certain food types (Borror et al., 1976; Roberts, 1978) than with the seasons. From this premise, Cary (1981) hypothesised that the seasonal species of wētā such as *Deinacrida rugosa* and *Pachyrhamma fascifer* may have a higher degree of food specificity than the non-seasonal ones such as *D. fallai, D. heteracantha* and *P. turneri.*

Most non-migratory insects in temperate climates, and many in seasonal tropical climates exhibit some form of dormancy during those seasons least favourable for growth, development and reproduction (Roberts, 1978). In general there are three strategies for winter dormancy: cold torpor, winter quiescence and winter diapause (Roberts, 1978). The former two strategies are similar responses to spells of unfavourable weather and differ only in duration. Cold torpor typically lasts for a few hours or days and is not seasonal, while winter quiescence lasts for the entire cold season. Diapause, however, is seasonally specific, persists for a set minimum period of time regardless of environmental conditions, and almost always occurs in one species-specific stage in the insects' life cycle (Roberts, 1977). The timing of diapause induction is under the control of hormones triggered by day length or some other extrinsic environmental factors, while torpor and winter quiescence are simply caused by temperature acting on the metabolic rate (Roberts, 1978). With regard to these criteria, the overwintering strategy of *Hemiandrus* new sp. is discussed.

Methods.

In the laboratory, all preserved wētā were sexed (where possible) and measured under a dissecting microscope. Hind femur length and inter-ocular distance were measured to the nearest 0.1mm (fig. 4.1). Previous workers have considered hind femur length as the most reliable indicator of wētā size, as it is the longest structure available and changes maximally between instars (Cary, 1981; Butts, 1983). Additionally, the ovipositor length (from the base of the sub-genital plate to the ovipositor's tip) (fig. 4.1) of third and later instar females was measured. The sex of first and second instar specimens was not usually discernable.

Live specimens were brought to the laboratory as soon after capture as possible, immobilized with CO_2 and measured as described above. The time wētā spent affected by CO_2 was minimized to reduce the risk of permanent damage from anaerobisis (W. Davison, pers. comm.).

Results and Discussion.

Plots of frequency against hind femur length (to the nearest 0.1 mm) for all females and all males show multi-modal distributions (figs. 4.2a and 4.2b respectively). The clumps are likely to represent the extent of the size range of each instar, with peaks being close to the mean (Cary, 1981). If

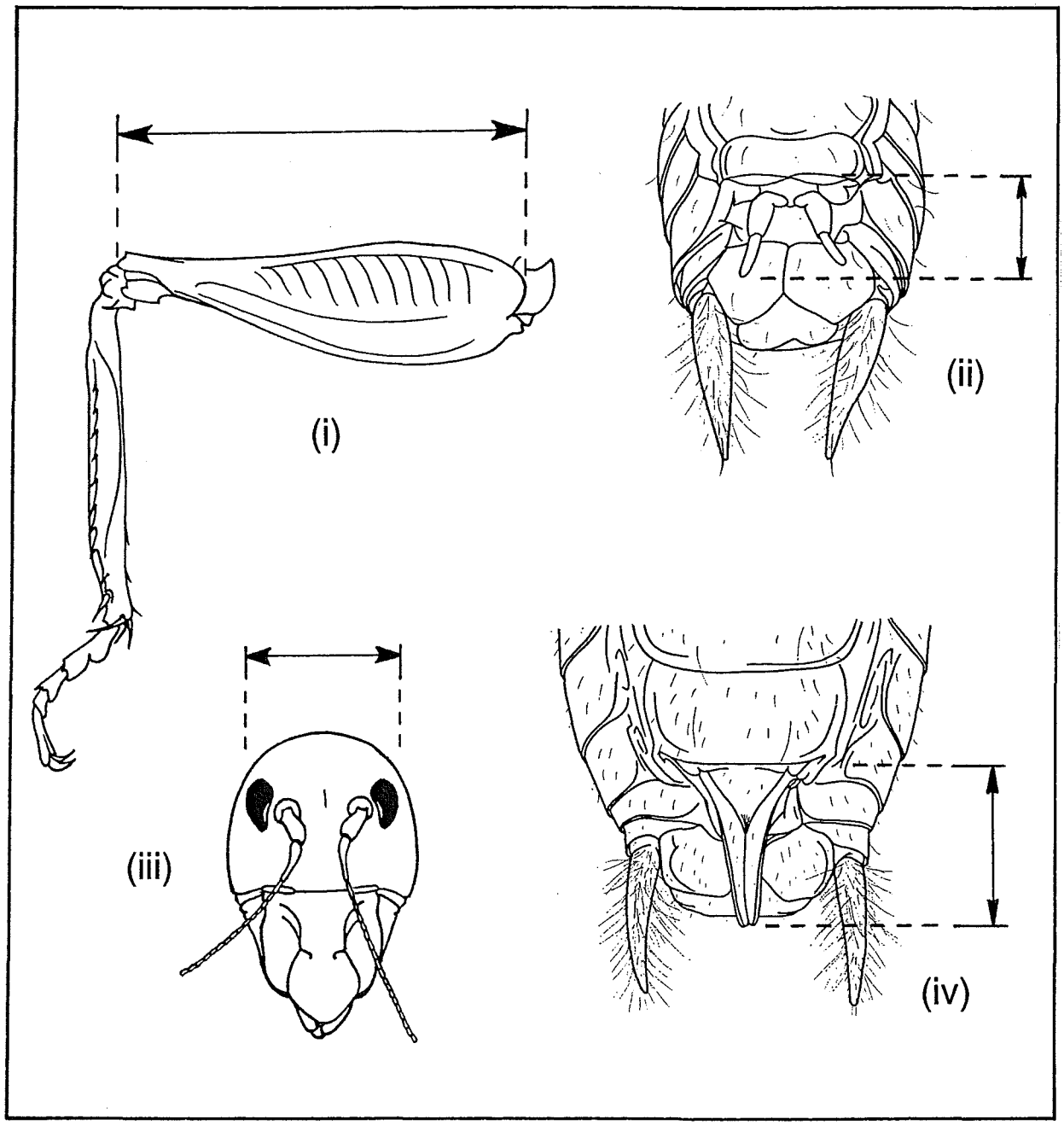

Figure 4.1. Measured structures of *Hemiandrus* new sp. (not to scale). (i) hind femur; (ii) ovipositor of early instar female; (iii) inter-ocular distance; (iv) ovipositor of late instar female.

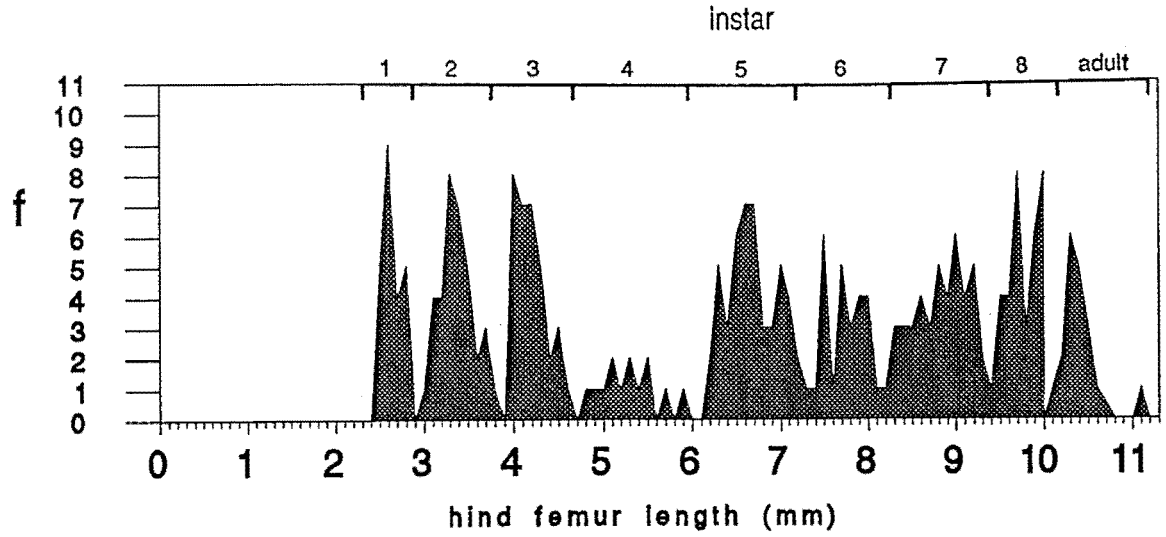

Figure 4.2a. Size frequency distribution of female *Hemiandrus* new sp.

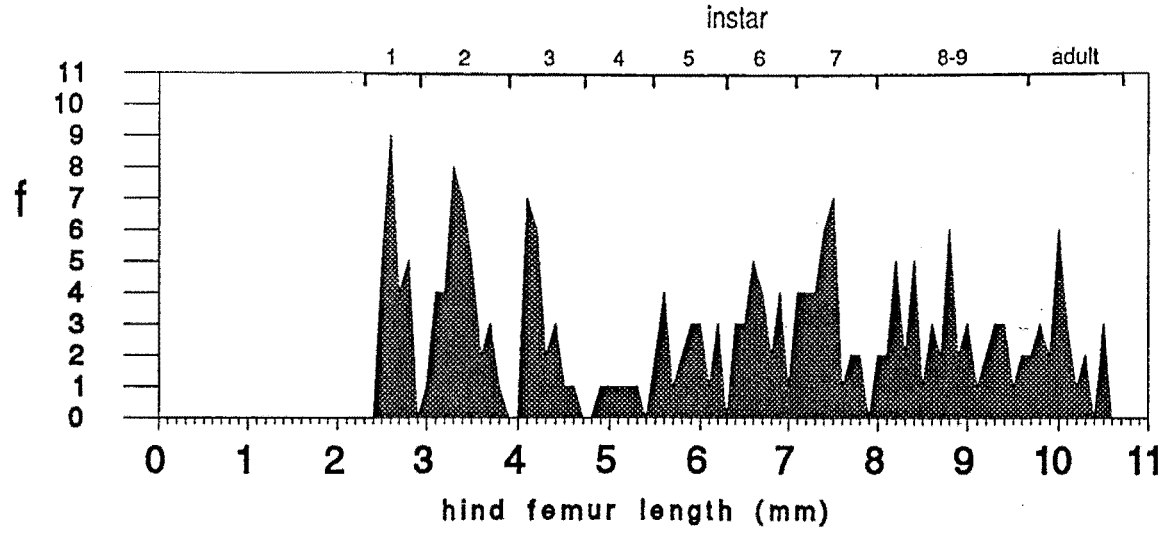

Figure 4.2b. Size frequency distribution of male *Hemiandrus* new sp.

similar frequency distributions are obtained from measurements of two or more structures, the instar groupings are more likely to be correct. However, frequency plots of inter-ocular distance for both sexes showed instar groupings less distinct than those of hind femur length. The inter-ocular distance is a much smaller value and measurement errors therefore relatively large. The resultant overlap between instar groups was such that only some instars for both sexes were clearly recognisable, and the graphs are not presented. The same problem occurred for the frequency plots of female ovipositor length, so this too is not considered a reliable indicator of instar group. Figure 4.2a (the frequency distribution of all female hind femur lengths) indicates that females have nine instars. The divisions represented on this graph are relatively clear, and supported both by measurements of captive specimens and differences in genitalia. Figure 4.2b (the frequency distribution of all male hind femur lengths) shows that male *Hemiandrus* sp. have ten instars. Instars eight, nine and ten are not clearly distinguished by the frequency distribution, but evidence from measurements of captive specimens, as well as differences in the appearance of the genitalia (see section B, this chapter) supported the divisions.

The numbers of instars reported here are within the known range for the Gryllacridoidea (Ramsay, 1964), but the difference between the sexes is unusual. Unlike most other species studied, the smaller of the sexes of *Hemiandrus* new sp. (male, see below) appears to develop through an extra instar.

In total 273 females and 224 males were measured. Measurements from all sexually undifferentiated individuals of instar one and two are included in figures 4.2a and 4.2b.

By plotting the occurrence of each 0.1mm size class trapped in each month of sampling, the appearance and growth of cohorts can be traced. Figure 4.3a shows the size classes of female wētā present at each month of sampling (October 1993 - January 1995). First instar nymphs appeared in November and December. Rapid growth over the first summer and autumn saw females reach instars four and five by winter. The second winter saw this cohort reach instars seven and eight, and the previous year's adults were also represented. Adult females were present throughout the year, indicating that they survive long after mating and oviposition. Evidence from laboratory held specimens indicated that females matured in early spring and died in early summer. Given that adult females were present all year round, they must have survived from spring to the summer of the following year. No laboratory held females survived long enough to confirm this deduction[11].

Figure 4.3b shows the size classes of males present at each month of sampling. After hatching in November and December, males grew to fourth and fifth instar by winter. No growth was apparent over winter, but by the following autumn, seventh to ninth instar males were most common (along

[11]Many wētā were maintained in the laboratory but development did not resemble that of wild cohorts. The longest lived individuals survived for 13 months, but after proceeding normally for a few months, growth generally ceased.

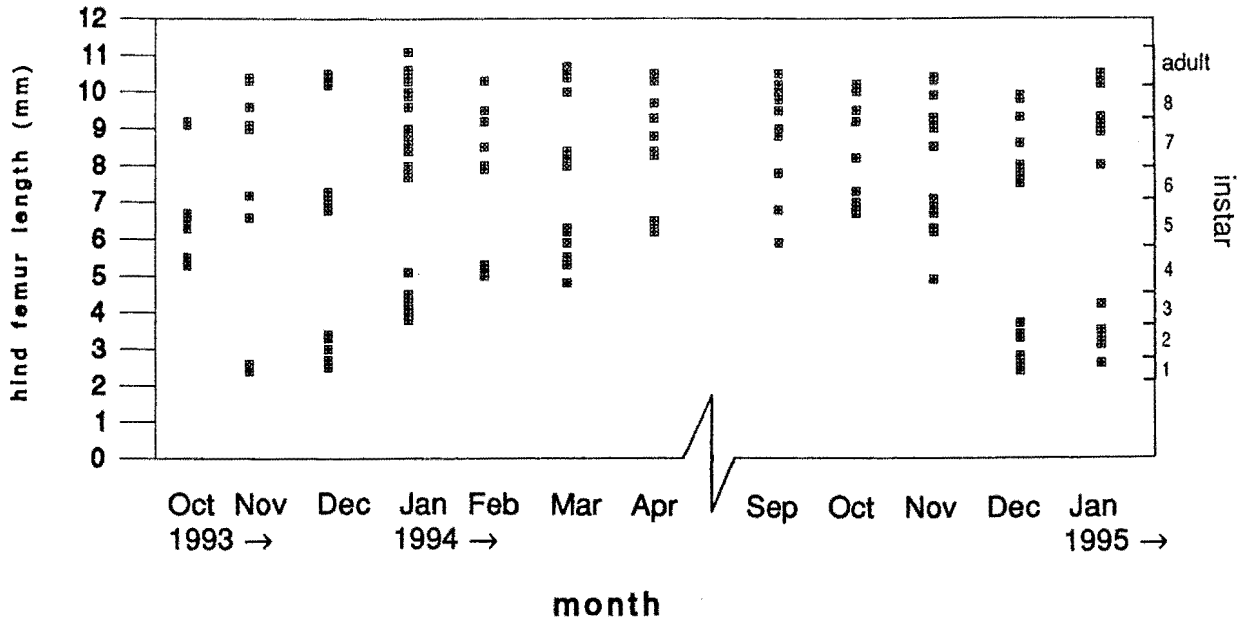

Figure 4.3a. Scatterplot showing the presence of 0.1mm size classes of female *Hemiandrus* new sp. each month. The winter months of May - August 1994 are omitted.

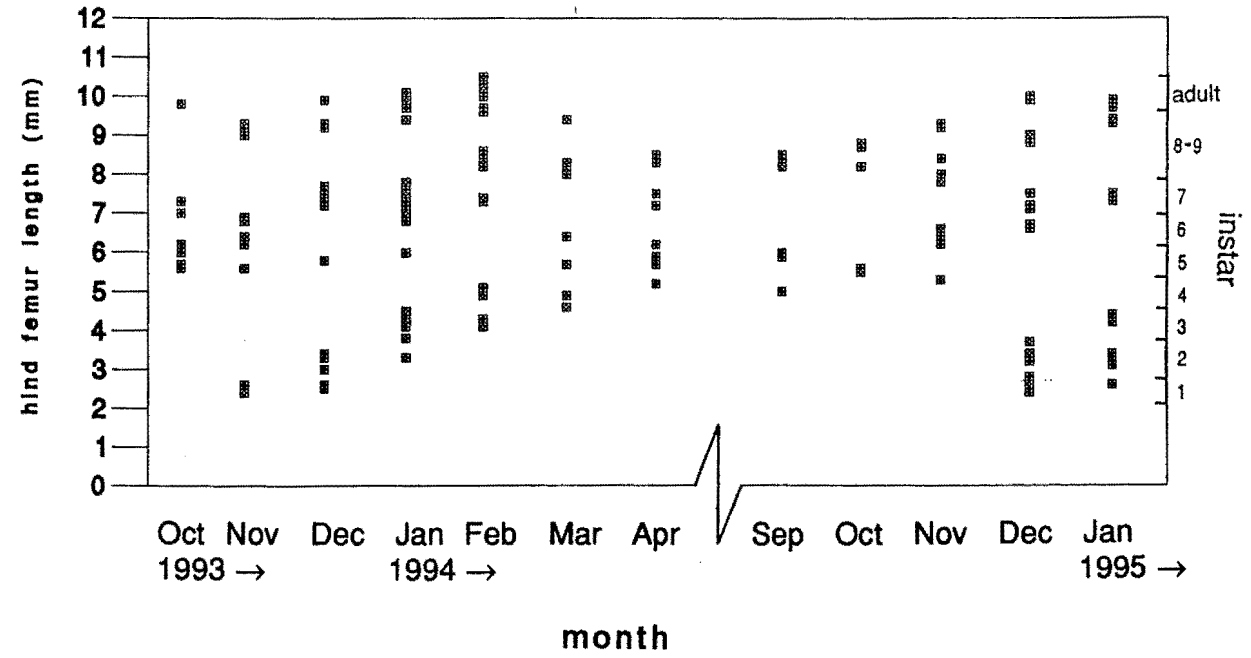

Figure 4.3b. Scatterplot showing the presence of 0.1mm size classes of male *Hemiandrus* new sp. each month. The winter months of May - August 1994 are omitted.

with the next generation of fourth and fifth instar nymphs). Again, these stages overwintered and adulthood was reached early in the third summer. By late summer, adult males were not recorded. Around this time most adult males held in the laboratory also died, so it is assumed that males, unlike females, do not survive past their third summer.

Laboratory specimens of *Hemiandrus* new sp. were observed stridulating during early summer, and although it was not observed, mating probably takes place then. This is the case for other species of *Hemiandrus* (J. Townsend, pers. comm.). Many adult females trapped in mid-summer were gravid, but few in late summer were, indicating that oviposition occurs in mid to late summer. An adult female and 36 eggs were found in a burrow in November (see chapter 6). Given that oviposition is most likely to occur in mid to late summer, the female clearly must have overwintered with the eggs.

Figures 4.4a and 4.4b are diagrammatic representations of the life cycles of female and male *Hemiandrus* new sp. respectively. Each semi-circle extends over the part of the year that the greatest numbers of that instar were recorded. Figure 4.4b shows, for example, that both fourth and fifth instar males were present during the cohort's first winter. As the same instar groups were present before and after the winter period (when no sampling was undertaken), it is likely that minimal growth occurred during this time.

Hemiandrus new sp. has a developmental cycle strongly linked to the seasons, a feature not surprising for a species inhabiting an area with seasonal climate extremes (Cary, 1981). No wētā were trapped during the winter sample (June 1994), and very few in April and September 1994, indicating that the species is inactive during these months. Undisturbed laboratory held specimens of *Hemiandrus* new sp. (kept at room temperature) were sometimes active during the winter, indicating that the overwintering strategy of this species is not a diapause. Insects in diapause will remain dormant regardless of external environmental conditions (such as temperature) for a pre-determined period (Roberts, 1978). It therefore seems likely that this wētā exhibits winter quiescence during the cold season.

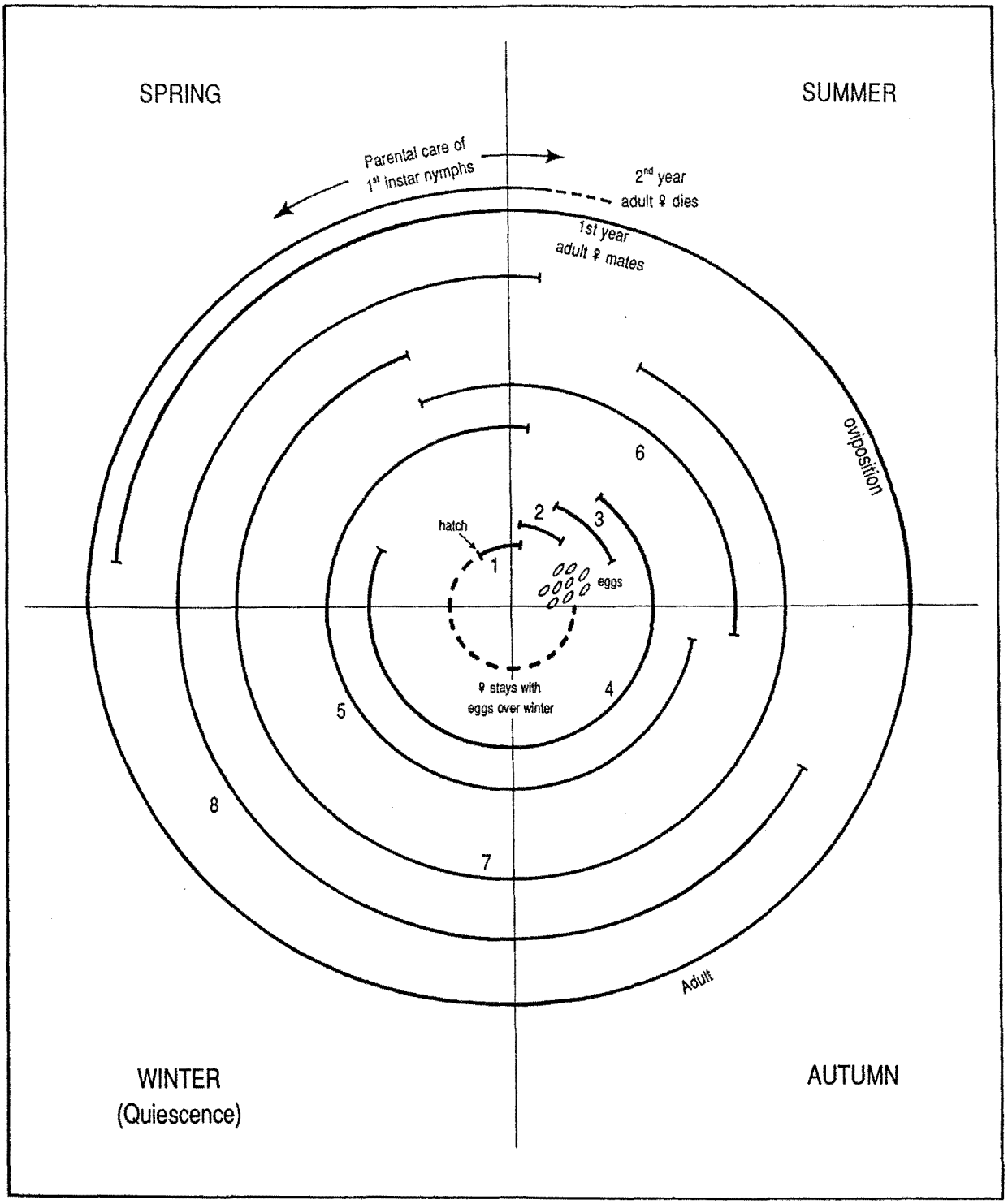

Figure 4.4a. Diagram of the life cycle of female *Hemiandrus* new sp., indicating the temporal extent of each instar (semicircles labelled with instar numbers) and important events.

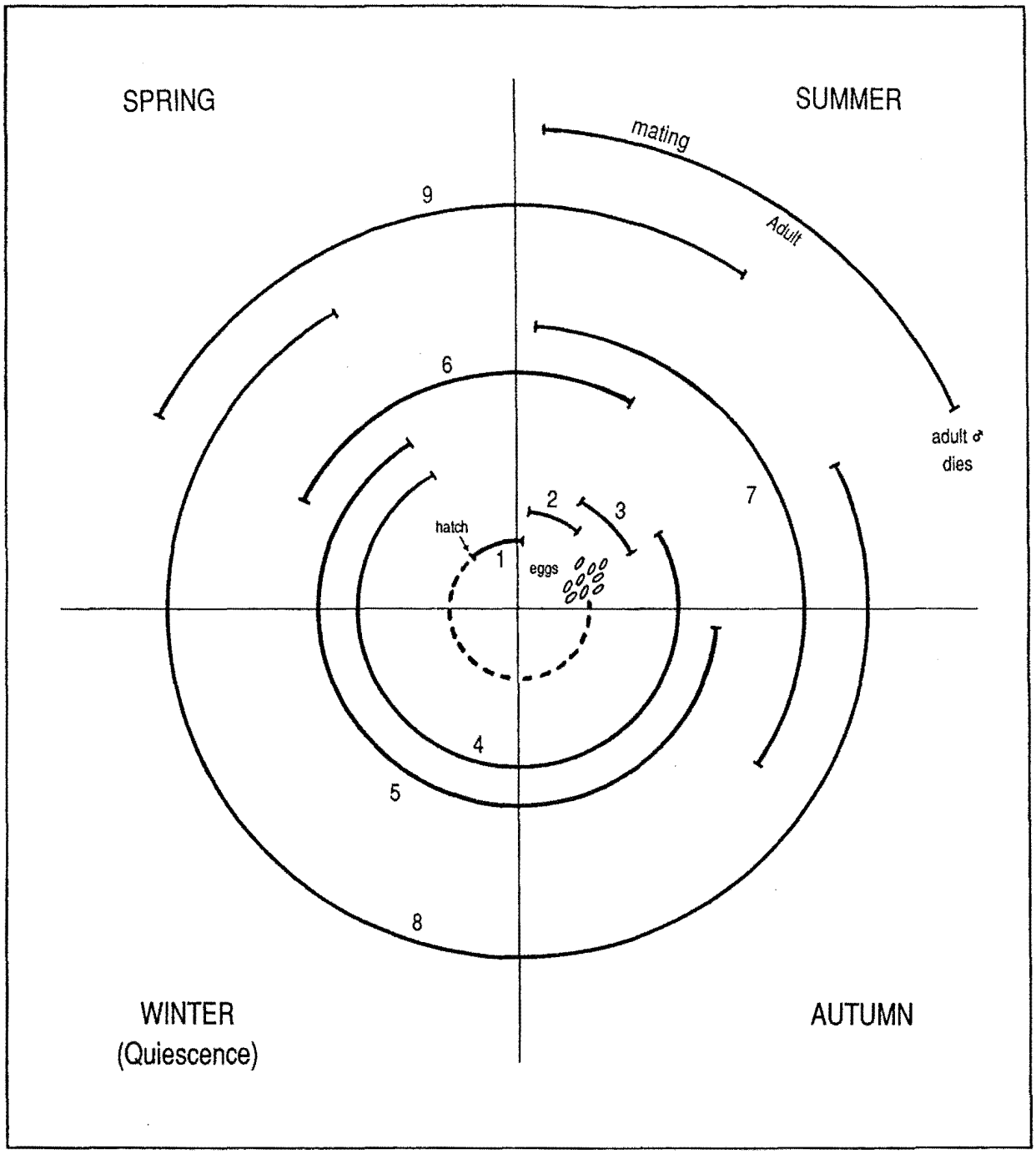

Figure 4.4b. Diagram of the life cycle of male *Hemiandrus* new sp., indicating the temporal extent of each instar (semicircles labelled with instar numbers) and important events.

B. Development of terminalia.

Introduction.

An insect's abdominal segments posterior from the 8th or 9th are usually modified for sexual and excretory functions and are known as terminalia (Naumann, 1991). The genitalia (often the most significant structures of the terminalia) can be very different between otherwise similar species, (especially those of the males), so are invaluable in taxonomic work (Davies, 1988).

Generally, genital appendages or gonopods are paired and each develops from a coxite (or gonocoxa) with an apical style (or gonostylus). The male gonopods develop from the 9th abdominal segment while those of the female develop from the 8th and 9th (Davies, 1988), but structures from other segments may be sexually differentiated (Tuxen, 1970).

Methods.

The terminalia of selected instars of male and female wētā were drawn using a dissecting microscope at 100-250 x magnification. As the sexes of first and second instar wētā were not distinguishable (except for a few specimens with unusually advanced development)[12], they have been drawn only once. Only whole specimens were drawn and each figure was drawn from a single specimen selected from the centre of that instar's estimated size range, and checked by comparison with several other similar sized specimens.

Results and Discussion.

The following are brief descriptions of major new features present at each of the presented instars.

1st and 2nd instar nymphs.

Figure 4.5(i) shows that the 1st instar nymphs bear a pair of gonopods ventrally on the 9th segment. The coxites and styles are considerably larger and more well defined in the 2nd instar (fig. 4.5(ii)).

Female, 3rd instar.

The coxites and styles of the previous undifferentiated instar (fig. 4.5(ii)) have now become what are clearly the paired 3rd valves of the ovipositor (one of two pairs of valves arising from the 9th abdominal segment) (fig. 4.6a(i)). The ventral surface of segment 9 is reduced in size. The styles are shorter and narrower.

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[12]Alternatively these may have been very small third instar specimens, as instars were grouped primarily by size, not sexual development.

Female, 4th instar.

The 8th sternite has now become reduced and appearing beneath its posterior surface are the 1st and 2nd paired valves, arising from the 8th and 9th abdominal segments respectively. The coxite of the 3rd valve is larger and the style much reduced from the previous instar (fig. 4.6a(ii)).

Female, 6th instar.

By this stage, the 8th sternite is no longer obvious. A small sub-genital plate has begun to develop between the coxites of the first pair of valves. The valves now resemble an ovipositor. The 1st and 3rd valves have completely enclosed the 2nd valves. Styles are still present on the 3rd valves (fig. 4.6b(i)).

Female, 8th instar.

The ovipositor is now longer than the cerci and 1st and 3rd valves are of equal length. The sub-genital plate is enlarged and triangular, with a partially sclerotized posterior tip (fig. 4.6b(ii)).

Female, 9th instar (adult).

The adult female bears an enlarged 7th sternite with a scalloped posterior margin. The sub-genital plate extends anteriorly to this margin, and its posterior tip is strongly sclerotized. The 3rd valves are slightly longer than the 1st and the tips of both pairs are lightly sclerotized. Sensory hairs are present sparsely on the ovipositor and much of the body, but densely on the cerci (fig. 4.6c).

Male, 3rd instar.

This stage is similar to the undifferentiated 2nd instar, but an obvious hypandrium is formed from the 9th sternite fused with the coxae of the 9th segment. The styles are large and bear fine sensory hairs as do the cerci (fig. 4.7a(i)).

Male, 4th - 9th instars.

Details of instars 4 (fig. 4.7a(ii)), 7 (fig. 4.7b) and 9 (fig. 4.7c) are presented. The most significant changes to the terminalia over these instars, apart from the increase in size, is the extension of the lobes or processes of the paraprocts, first visible as small posterior outgrowths of the inner edges of the paraprocts in the 4th instar (fig. 4.7a (ii)). The styles are progressively reduced in size relative to the hypandrium. By the 9th instar the processes of the paraprocts are greatly increased in length but remain apically rounded (fig. 4.7c). In the lateral view (fig 4.7c(i)), the 10th tergite shows the beginning of a paired dorso-lateral modification.

Male 10th instar (adult).

There are significant developments from the 9th instar to the adult male. The lobes of the paraprocts are now apically pointed, partially hollowed and sclerotized. The 10th tergite is reduced and partially fused with the epiproct, and its modifications have become hard sclerotized hooks. The adult cerci

are curved upwards and slightly inward unlike all sub-adult males in which they are straight. The hypandrium has extended to cover most of the basal parts of the paraprocts. Sensory hairs are present sparsely over much of the body surface, but most densely around the margins of the hypandrium and on the cerci (fig. 4.7d).

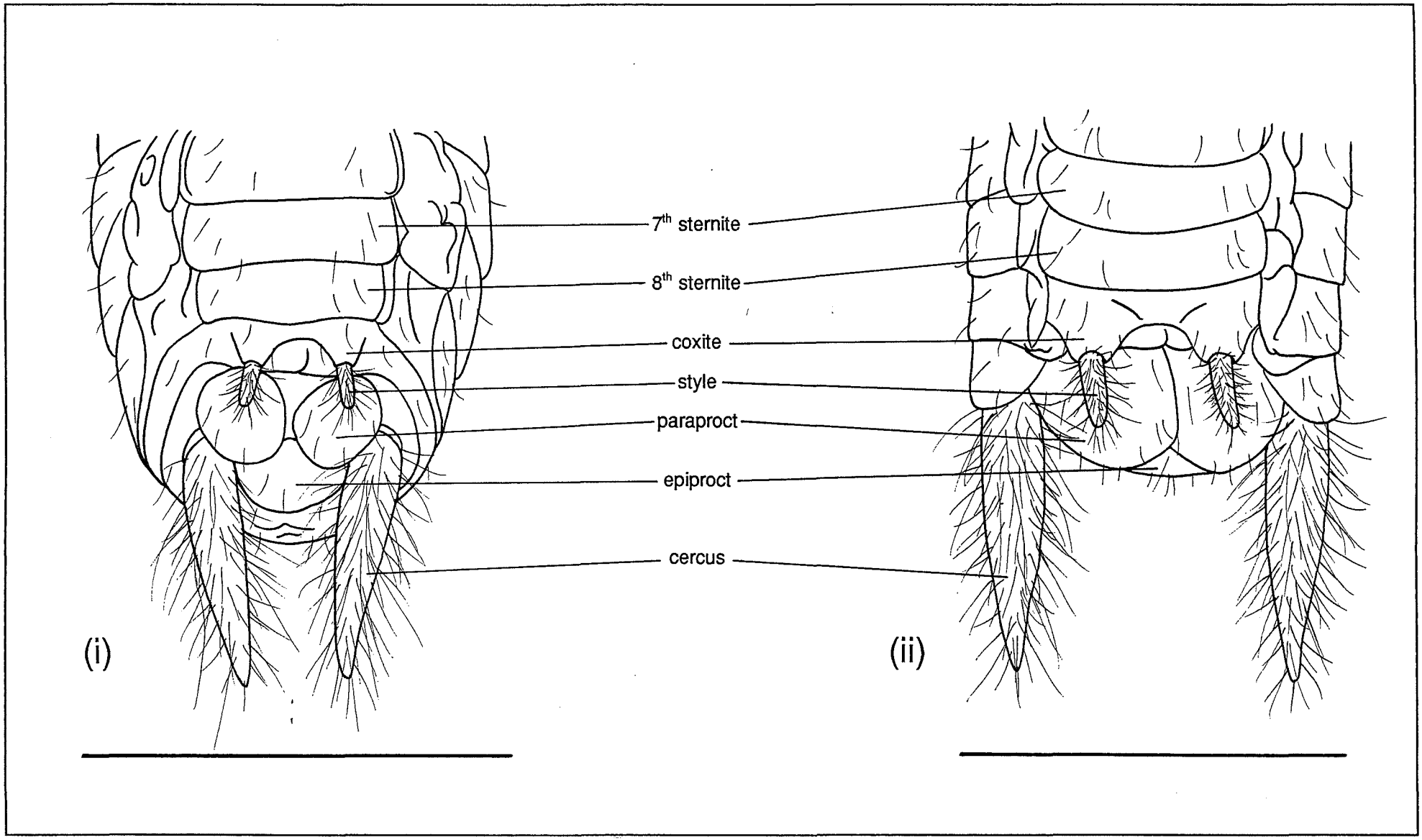

Figure 4.5. Terminalia of *Hemiandrus* new sp. (i) 1st instar, ventral view, (ii) 2nd instar, ventral view. Scale bars = 1mm.

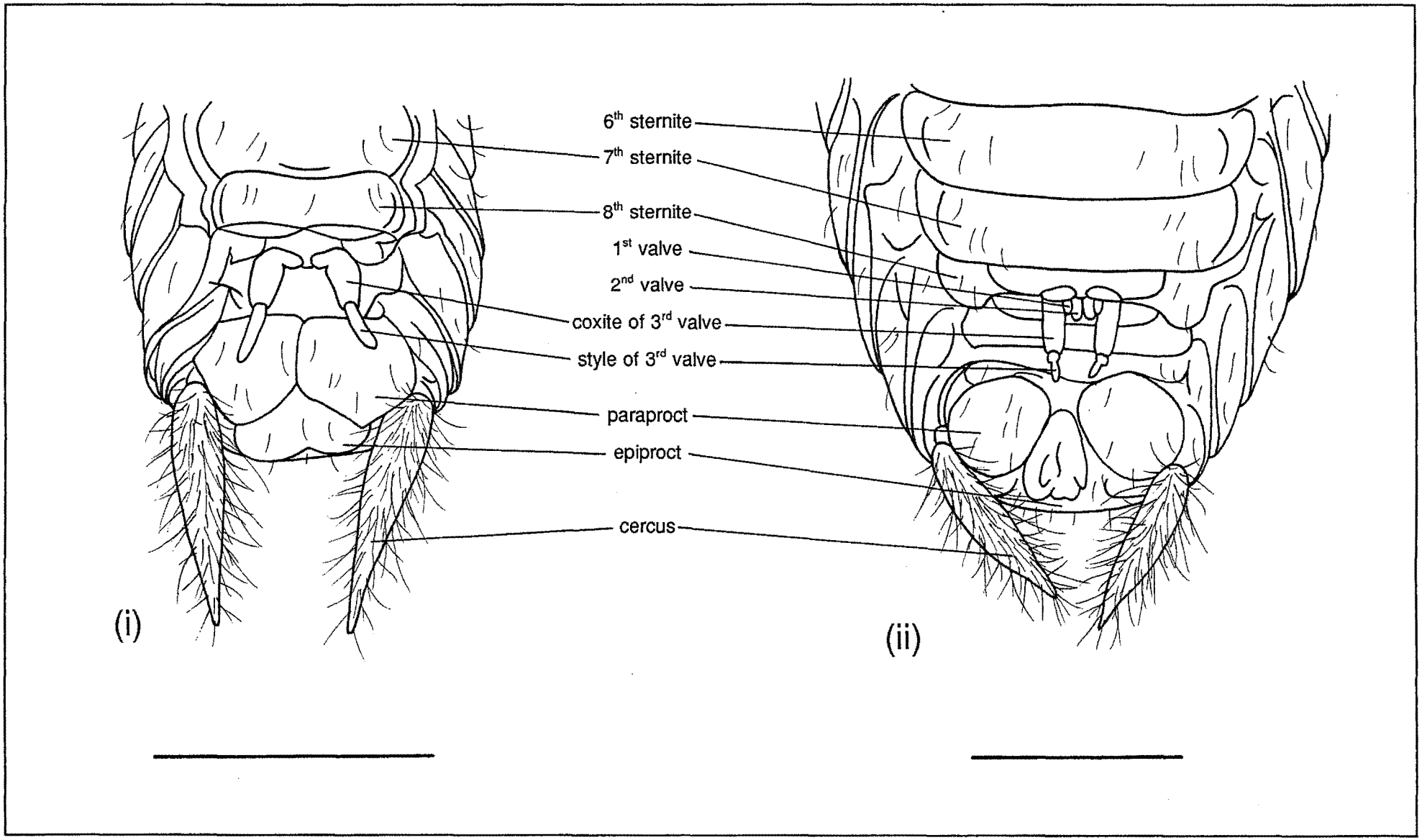

Figure 4.6a. Terminalia of female *Hemiandrus* new sp. (i) 3rd instar, ventral view, (ii) 4th instar, ventral view. Scale bars = 1mm.

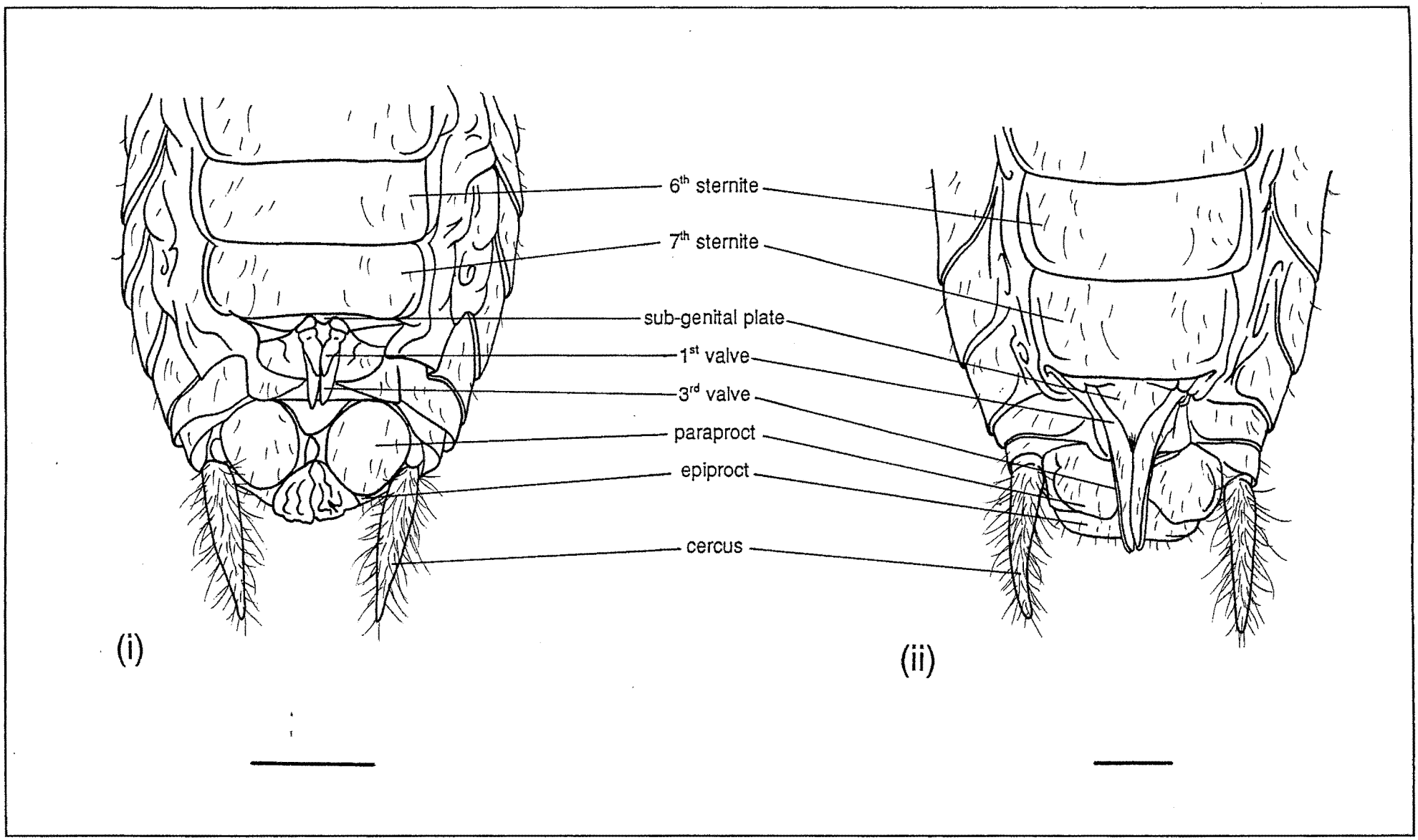

Figure 4.6b. Terminalia of female *Hemiandrus* new sp. (i) 6th instar, ventral view, (ii) 8th instar, ventral view. Scale bars = 1mm.

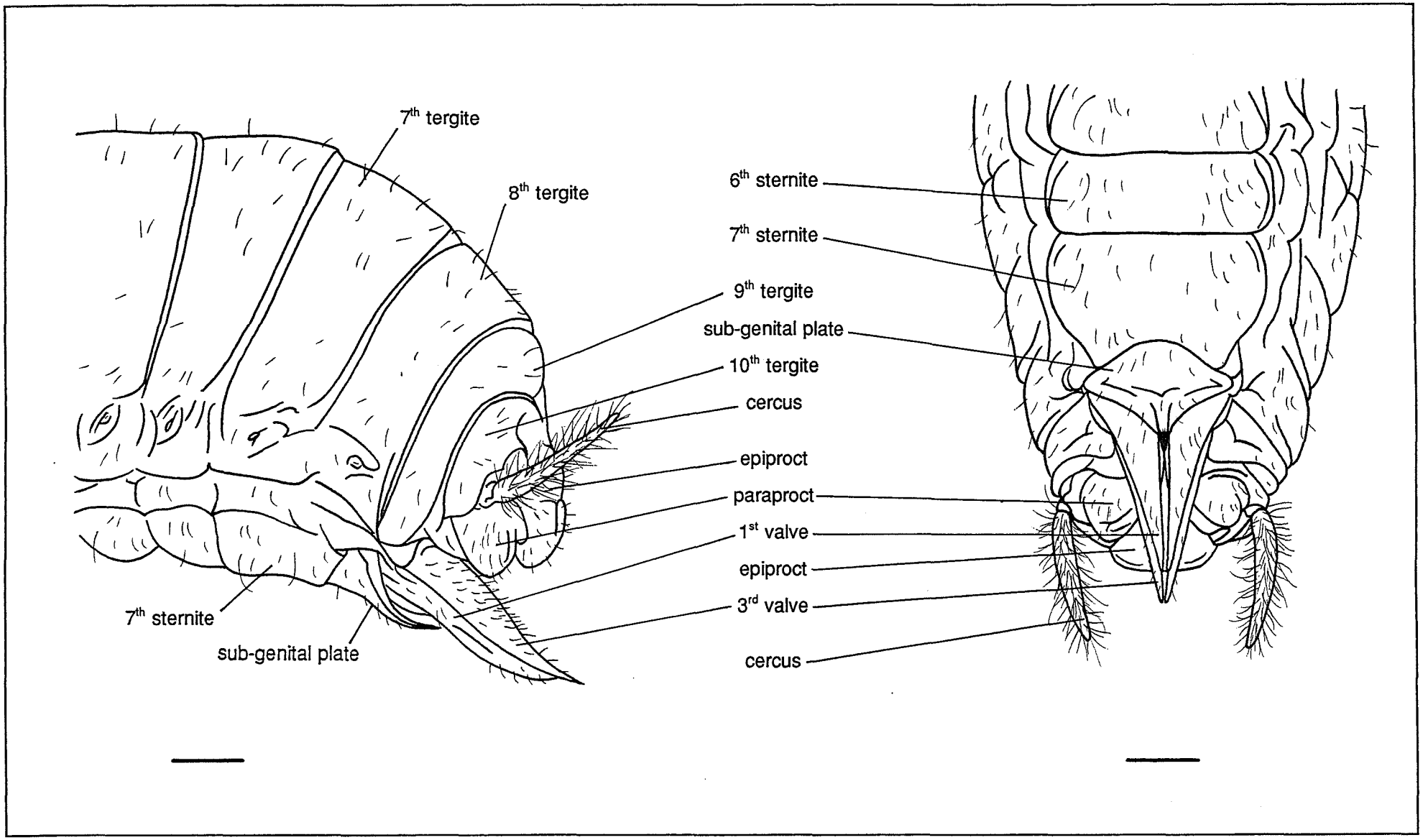

Figure 4.6c. Terminalia of female *Hemiandrus* new sp. (i) adult, lateral view, (ii) adult, ventral view. Scale bars = 1mm.

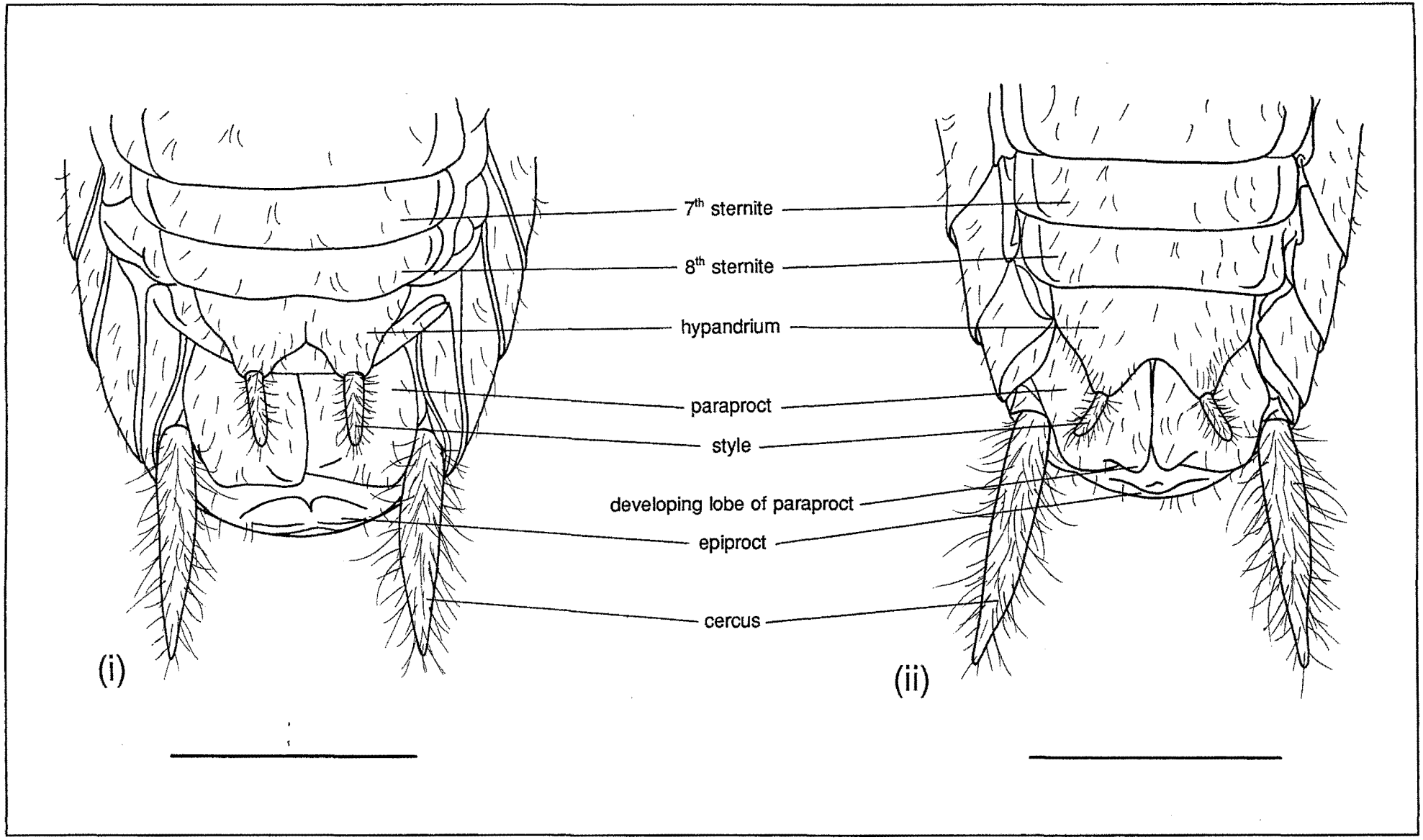

Figure 4.7a. Terminalia of male *Hemiandrus* new sp. (i) 3rd instar, ventral view, (ii) 4th instar, ventral view. Scale bars = 1mm.

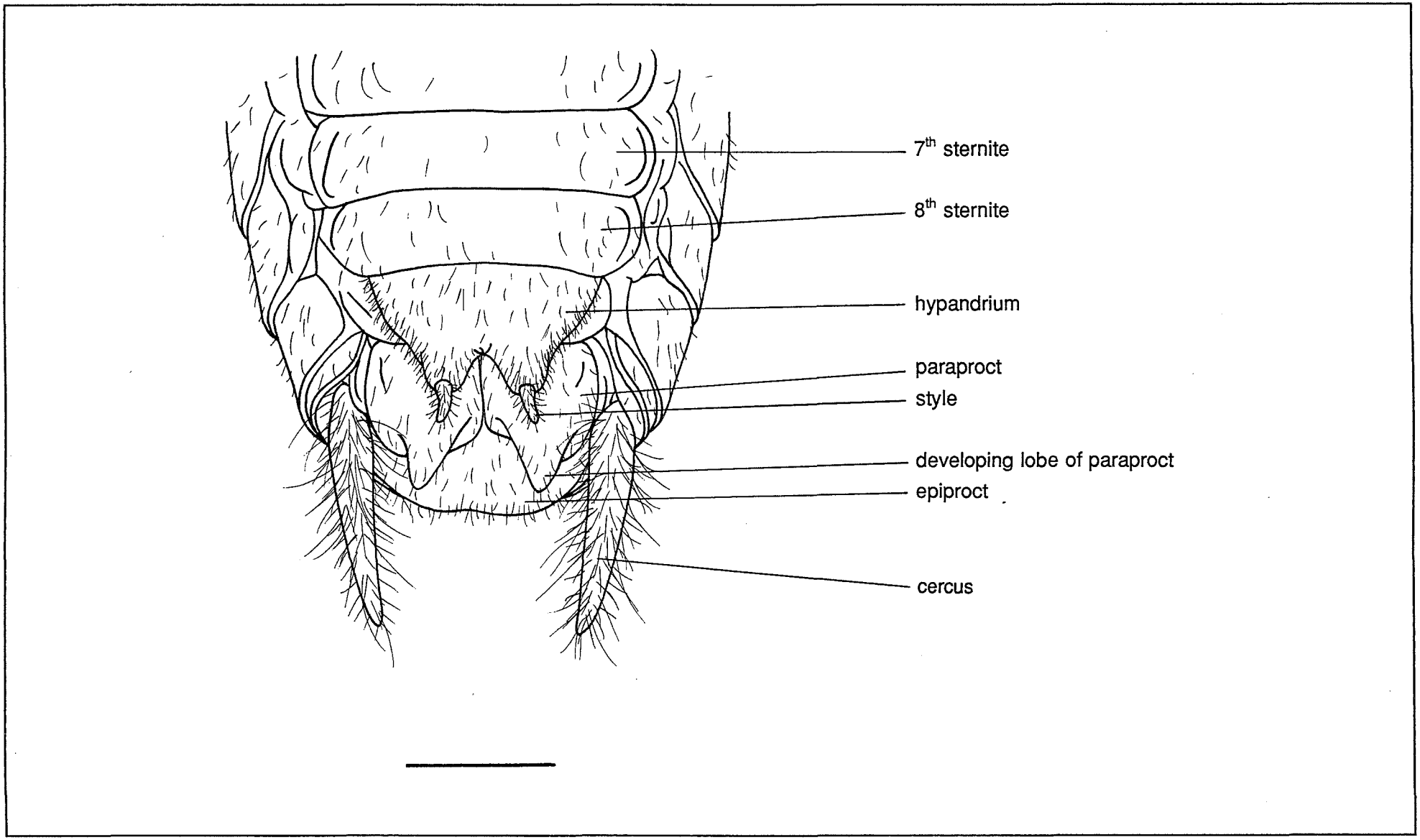

Figure 4.7b. Terminalia of male *Hemiandrus* new sp., 7th instar, ventral view. Scale bar = 1mm.

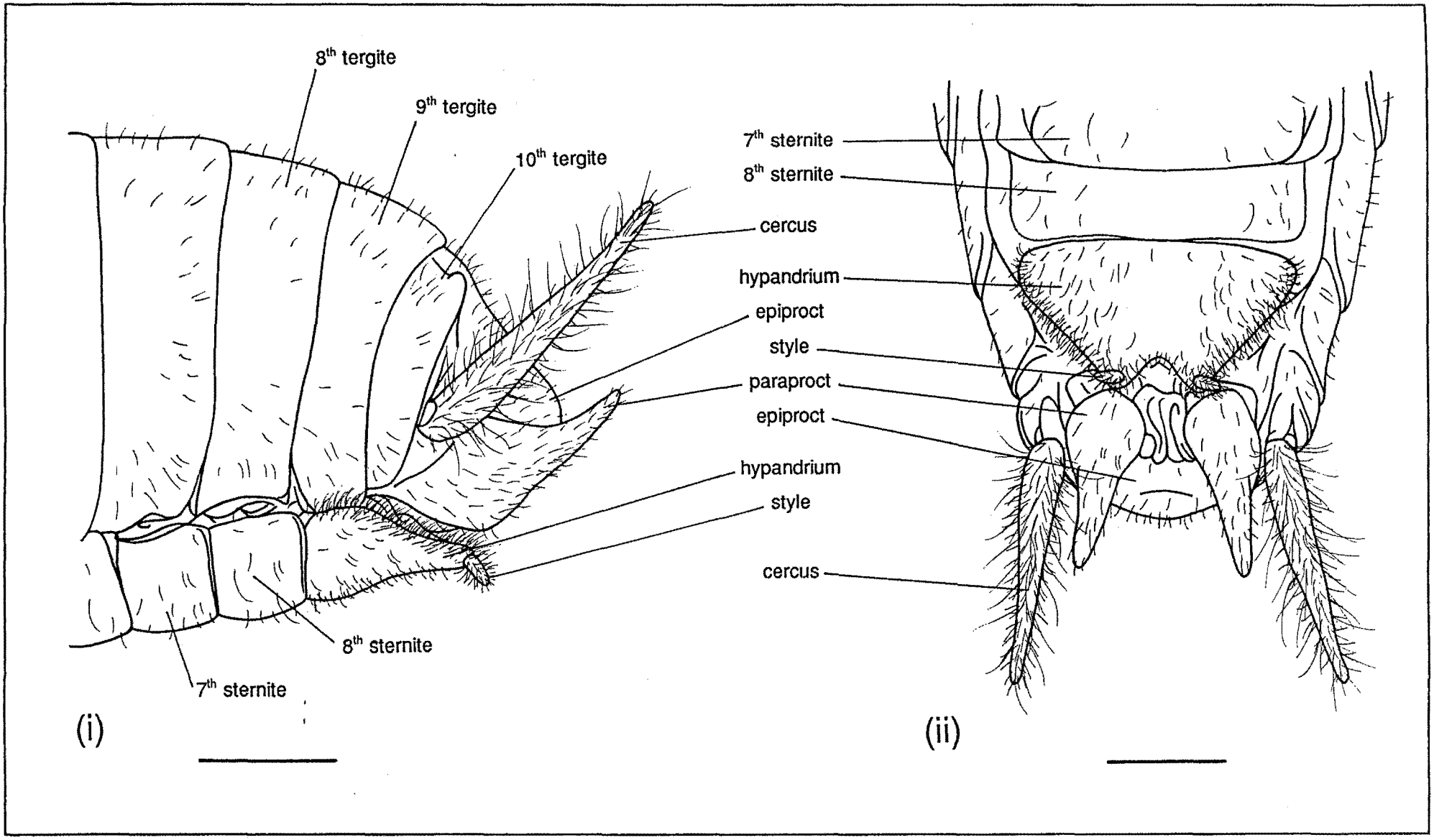

Figure 4.7c. Terminalia of male *Hemiandrus* new sp. (i) 9th instar, lateral view, (ii) 9th instar, ventral view. Scale bars = 1mm.

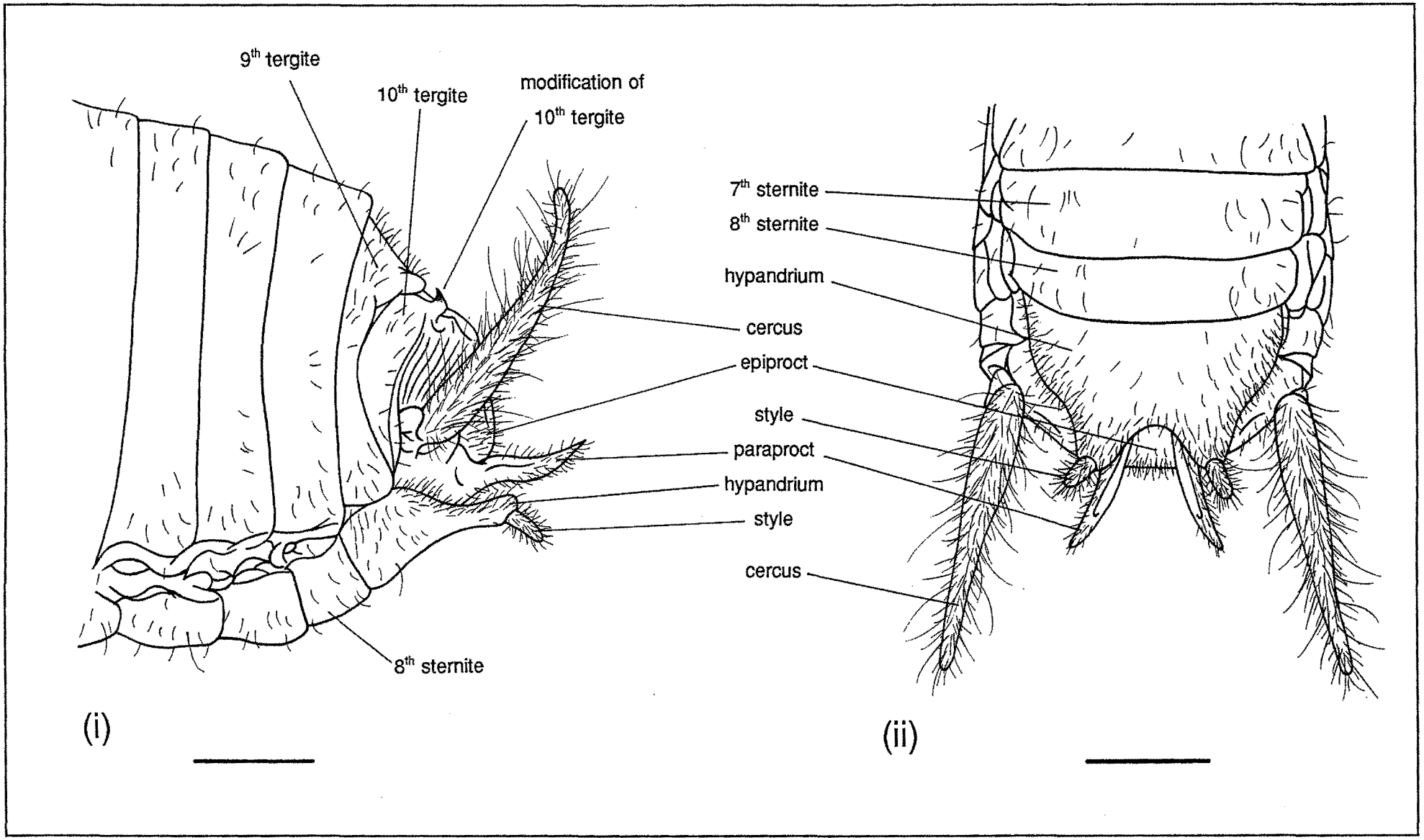

Figure 4.7d. Terminalia of male *Hemiandrus* new sp. (i) adult, lateral view, (ii) adult, ventral view. Scale bars = 1mm.

C. Comparison of the Cromwell and Tekapo species.

Introduction.

P. M. Johns (pers. comm.) considers the Cromwell and Tekapo wētā to be sufficiently different to be classified as separate species. The purpose of this section was to identify consistent characteristics from which the distinction could be made.

There were very few adult Cromwell *Hemiandrus* sp. available for study (four males and one female). One of the males was considerably smaller in all dimensions than the other three and may have been abnormal, so was not included as part of the sample.

Genital and other characteristics, and mean dimensions of the Cromwell wētā samples were compared to those of samples of the Tekapo wētā to find distinguishing features.

Methods.

a. Tibial spines. There are two rows of lateral spines on the hind tibiae of both taxa. Numbers and extent of these in adults of both samples were compared.

b. Terminalia. The appearance of both adult male and adult female genitalia were compared between the taxa. The single female Cromwell wētā included in the following tests was considered to be an adult. The shape, sclerotization and pointed valve tips of the ovipositor were adult-like, as were the enlarged 7th sternite (relative to the other sternites) and the broad sub-genital plate (fig. 4.8).

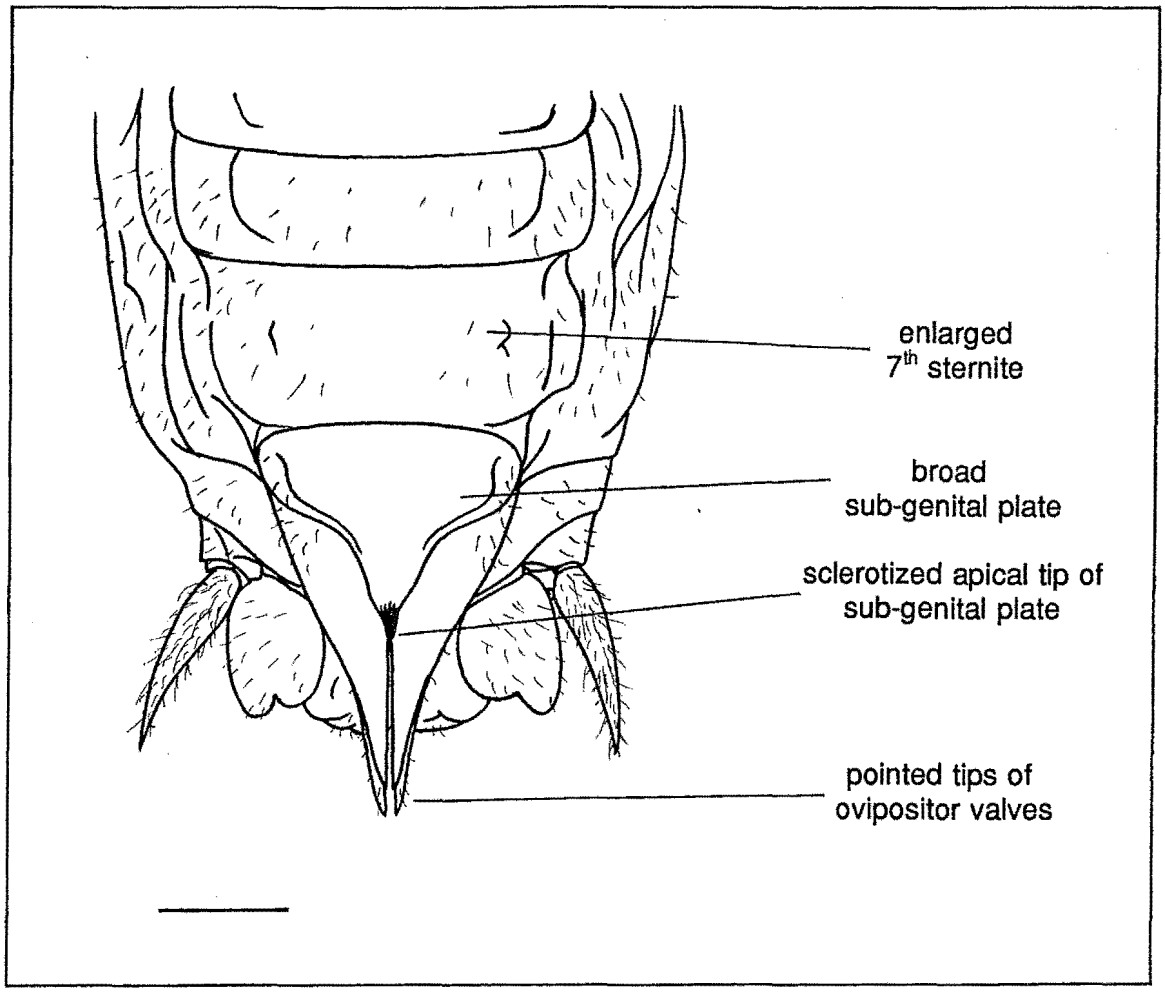

Figure 4.8. Terminalia of adult female Cromwell *Hemiandrus* sp. (ventral view), showing adult-like features (compare with adult female Tekapo species (fig. 4.6c)). Scale bar = 1mm.

c. Morphometrics.

(i) Female. Using the *t*-test for the comparison of a single observation with the mean of a sample (Sokal and Rohlf, 1981), several dimensions of the Cromwell wētā female were compared to means of those of a randomly selected sample of adult Tekapo wētā females (n = 20). The dimensions were hind femur length (as an indicator of overall body size), inter-ocular distance (I.O.D.), ovipositor length, cercus length, the ratio of hind femur length to ovipositor length and the ratio of hind femur length to inter-ocular distance.

As the overall size and ovipositor length (though not ovipositor shape) of the Cromwell female appeared more similar to those of penultimate (8^{th}) instar female Tekapo wētā than to adults, the same series of tests was repeated using a randomly selected sample of 8^{th} instar Tekapo wētā females (n = 28).

(ii) Male. Mean dimensions of the sample of adult male Cromwell wētā (n = 3) were compared to those of a randomly selected sample of adult male Tekapo wētā (n = 21). The means of hind femur length, inter-ocular distance (I.O.D.), cercus length, the ratio of hind femur length to inter-ocular distance and the ratio of hind femur length to cercus length were calculated. By constructing confidence intervals for the difference between the means of the samples, the significance of the differences can be established (Ott and Mendenhall, 1985).

Results.

a. Tibial spines. The hind tibiae of adult Cromwell and Tekapo wētā bear different numbers and arrangements of lateral tibial spines. The Tekapo wētā's tibiae have two nearly symmetrical rows of 7 - 10 (usually 8) spines extending three quarters of the way from the apical to the proximal end. The hind tibiae of the Cromwell wētā bear two less well defined rows of 5 - 8 (usually 6 or 7) smaller spines extending one half to three quarters of the way from the apical to the proximal end (fig. 4.9).

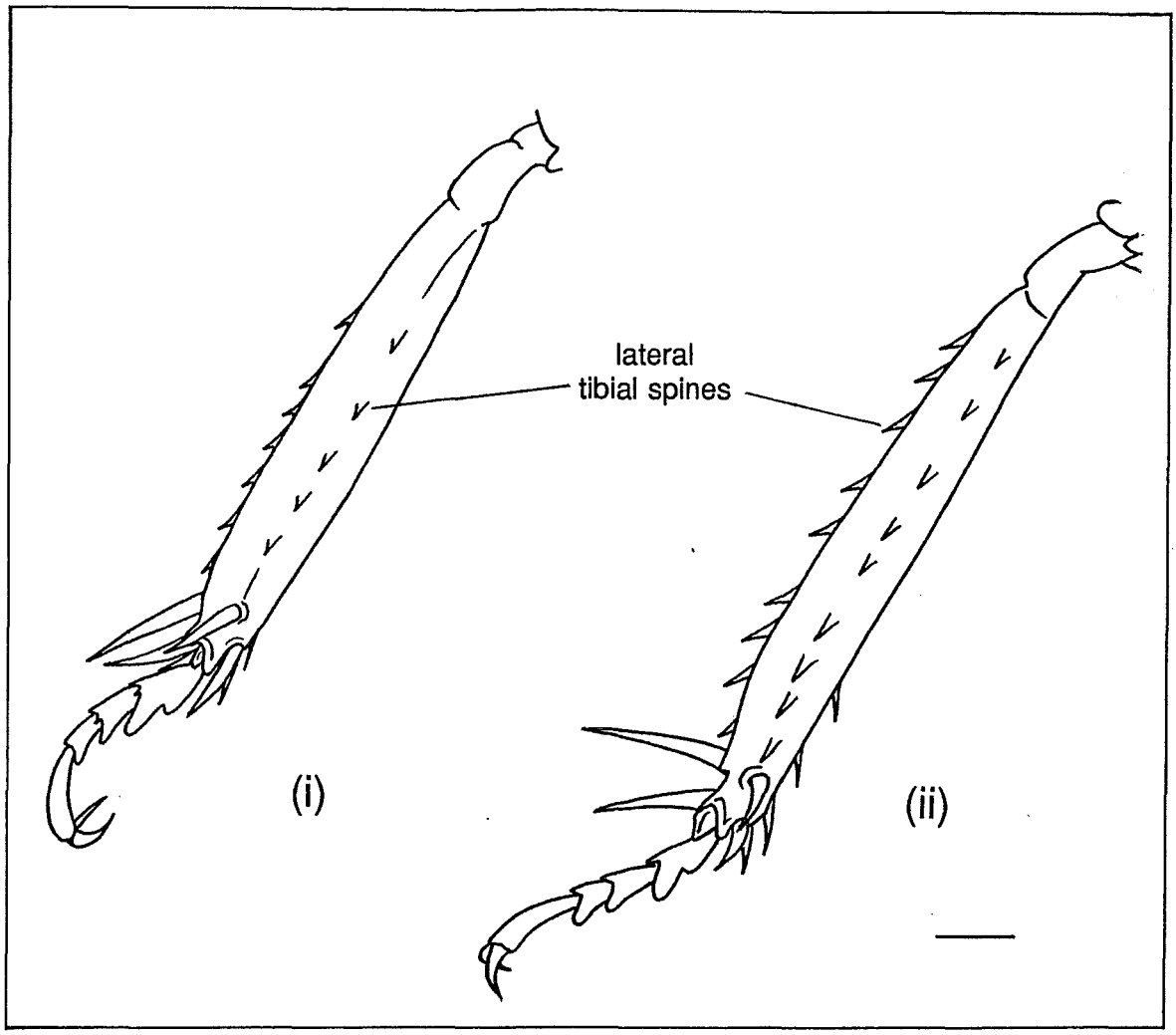

Figure 4.9. Hind tibiae (right legs) of adult (i) Cromwell, and (ii) Tekapo *Hemiandrus* spp., showing differences in lateral tibial spines. Scale bar = 1mm.

b. Terminalia. While the genitalia of male wētā of the two taxa are very similar, those of the females are not. The ovipositor is smaller, broader and the sub-genital plate and 7th sternite are different shapes (fig. 4.8; compare with Tekapo species (fig. 4.6c)).

c. Morphometrics.

(i) Female. The results of the *t*-tests for the comparison of a single observation with the mean of a sample are presented in table 4.1a.

The female Cromwell wētā was significantly different to the adult Tekapo wētā sample in the following dimensions: hind femur length, inter-ocular distance, cercus length, ovipositor length and hind femur length to ovipositor length ratio. Additionally, the Cromwell individual was significantly different to the 8th instar Tekapo wētā sample in the following dimensions: inter-ocular distance, cercus length, ovipositor length and hind femur length to ovipositor length ratio.

Table 4.1a. Sample means and sample standard deviations of measurements and ratios comparing females of the Tekapo and Cromwell wētā. The significance of tests are given in the far right two columns. The first significance column (8th ♀) concerns the comparisons between the sample of female 8th instar Tekapo wētā and the single Cromwell adult female, while the second (adult ♀) concerns comparisons between the sample of female adult Tekapo wētā and the Cromwell individual. Those tests significant at $\alpha < 0.05$ are in bold type.

		Crom. adult ♀ (n = 1)	Tek. 8th ♀ (n = 28)	Tek. adult ♀ (n = 20)	significance (α)	
					8th ♀	adult ♀
hind femur length (mm)	$\bar{x}$ s	9.0	9.475 0.391	10.250 0.349	$\alpha > 0.05$	**$\alpha < 0.01$**
I.O.D. (mm)	$\bar{x}$ s	4.0	4.571 0.156	4.810 0.202	**$\alpha < 0.01$**	**$\alpha < 0.001$**
cercus length (mm)	$\bar{x}$ s	1.7	2.064 0.131	2.190 0.171	**$\alpha < 0.02$**	**$\alpha < 0.01$**
ovipositor length (mm)	$\bar{x}$ s	3.1	2.464 0.260	4.245 0.267	**$\alpha < 0.05$**	**$\alpha < 0.001$**
femur : I.O.D. ratio	$\bar{x}$ s	2.25	2.037 0.110	2.124 0.069	$\alpha > 0.05$	$\alpha > 0.05$
femur : ovi. ratio	$\bar{x}$ s	2.90	3.830 0.227	2.450 0.174	**$\alpha < 0.001$**	**$\alpha < 0.05$**

(ii) Male. The results of the comparisons between means of the sample measurements and the significance of the differences are presented in table 4.1b.

The means of the samples of male Cromwell and Tekapo wētā were significantly different for the following dimensions: hind femur length, cercus length and hind femur length to cercus length ratio.

Table 4.1b. Sample means and sample standard deviations of measurements and ratios comparing adult males of the Tekapo and Cromwell wētā. The significance of tests are given in the far right column; those significant at $\alpha<0.05$ are in bold type.

		Cromwell adult ♂ (n = 3)	Tekapo adult ♂ (n = 21)	significance (α)
hind femur length (mm)	$\bar{x}$ s	9.533 0.058	10.062 0.240	**$\alpha < 0.01$**
I.O.D. (mm)	$\bar{x}$ s	4.633 0.153	4.620 0.189	$\alpha > 0.05$
cercus length (mm)	$\bar{x}$ s	2.200 0.100	2.724 0.184	**$\alpha < 0.001$**
femur : I.O.D. ratio	$\bar{x}$ s	2.059 0.056	2.181 0.116	$\alpha > 0.05$
femur : cercus ratio	$\bar{x}$ s	4.339 0.176	3.704 0.241	**$\alpha < 0.001$**

Discussion.

It is very important for the taxonomic status of a species to be clarified before conservation work proceeds (Emberson, 1994). Taxonomic distinctiveness is one of the five criteria assessed when priorities are set for conservation action (Tisdall, 1994). In the present study it is essential that the Cromwell *Hemiandrus* sp. is not the same taxon as the Tekapo River wētā otherwise its status would be very different and any conservation effort misguided.

While in some ways the two taxa of wētā appear superficially alike, the above results demonstrate the fact that they are not from the same population. Not only absolute measurements but ratios of measurements differ significantly (sometimes highly) between the taxa indicating that the Cromwell wētā is not simply a smaller version of the Tekapo species, but a distinct entity.

Chapter 5
Feeding Ecology

Introduction.

Hemiandrus new sp. is a burrowing animal, but is cursorial and feeds on the surface. Direct qualitative data on feeding could not be recorded from nocturnal observation in the field as the wētā were very rarely seen despite searches, and generally disturbed when encountered. For this reason it was considered that an analysis of the crop contents of a sample of specimens would provide the best information on the natural diet of the species[13]. No attempt was made to analyze the contents of the mid gut. Material present here has passed through the proventriculus and has been partially digested, leading to great difficulties in identification of even general food categories (Fuller and Stewart, 1977).

Most early reports of wētā diet in New Zealand have been anecdotal. For example, Buller (1870) wrote that *Deinacrida heteracantha* "subsists on green leaves of trees and shrubs", and the same author (1895) wrote that *D.* (now *Hemideina*) *broughi* fed on "the heart of red birch (sic) trees". Hutton (1896) described New Zealand Stenopelmatidae in general as being "vegetable feeders", but noted that Australian members ate primarily "self caught insects".

Many later papers presented short accounts of what food types were used to sustain laboratory specimens. These include Maskell (1926) for *Hemideina thoracica,* Ramsay (1955) for *D. rugosa,* Richards (1973) for *D. heteracantha* and *D. fallai,* Field (1980) for *D. connectens,* Sandlant (1981) for *H. femorata,* O'Brien (1984) for *H. maori* and Ordish (1990) for *H. crassidens.* The natural diets of wētā have been little investigated as most early papers focused on systematics, and later ones on aspects of behaviour.

The earliest non-anecdotal study of a wētā diet in New Zealand was that by Richards (1954) on the cave wētā *Macropathus filifer.* She investigated the food types utilized by both wild and laboratory animals. Contents of both gut (including crops) and faeces showed a diet incorporating leaves, grass, fungal spores, insect eggs and arthropods.

Crop content analyses have been used in a few other studies to determine diets of New Zealand Orthoptera. The technique can be particularly useful for omnivorous or carnivorous species, as it is usually easier to identify fragments of animal matter (such as arthropod exoskeleton) from a crop

[13]Little (1980) utilised faeces analyses to help determine the natural diets of two species of tree wētā (*Hemideina maori* and *H. femorata*) from Canterbury. This was necessary as large numbers of animals were not available for dissection. Unlike crop content analysis, faeces analysis does not require the death of the specimens.

than any form of plant material (Wahid, 1978; Cary, 1981)[14].

Ramsay (1955) concluded that *Deinacrida rugosa* (the Cook Strait giant wētā) was primarily a herbivore, eating a variety of dicotyledons, monocotyledons, mosses and ferns. This was based, however, on the crop contents of a single male, and is therefore unlikely to be a comprehensive representation of the diet of the species. Indeed, *D. rugosa* was found to prefer fresh meat in the laboratory (Ramsay, 1955).

From comparisons of faecal pellet constitution, Little (1980) concluded that while the tree wētā *Hemideina femorata* was almost entirely herbivorous, *H. maori* ate both plants and insects. She considered the difference to be related to the wētā's respective habitats. *Hemideina femorata* is a forest species and therefore has access to plentiful and diverse vegetation. *Hemideina maori* is adapted to a higher altitude habitat with a lower diversity of vegetation, so may compensate for the lack of variety by being an omnivore. Animal food is generally of higher nutritional value than plant food, and the assimilation efficiency is very high. Additionally, a ground living species such as *H. maori* may have access to more prey insects than a tree living species (Little, 1980).

While tree wētā are generally herbivorous or omnivorous, at least some species of ground wētā are almost entirely carnivorous (Cary, 1981). An analysis of the crops of *Zealandosandrus gracilis* from forests in the foothills of north-west Canterbury indicated that it fed predominantly on invertebrates of leaf litter and soil, especially Coleoptera and Lepidoptera larvae (Cary, 1981). There were no significant differences between the diets of males and females, nor between those of different nymphal stages.

Wahid (1978), examining crop contents, found that *Hemiandrus* sp. from a Canterbury apricot orchard showed important differences in food preferences between the sexes. While males ate mostly leaves and grasses, females preferred the apricots (in season). This difference was most marked in adults, younger wētā all eating foliage rather than fruit.

Butts (1983) examined the crops of samples of two Snares Island wētā species, the stenopelmatid *Zealandosandrus subantarcticus* and the rhaphidophorid *Insulanoplectron spinosum.* Males and females of the former species had similar diets, but they varied with age. First instar nymphs appeared to eat almost entirely animal matter, while second instar nymphs ate less than 10%. From the second instar there was a steady increase in animal matter consumption up to about 50% at adulthood. *Insulanoplectron spinosum* showed a far less regular pattern. There were no obvious

[14]Little (1980) was able to identify several plant species including manuka (*Leptospermum scoparium),* kanuka (*Kunzea ericioides*) and black beech (*Nothofagus solandri*) from faecal pellets of the two wētā *Hemideina maori* and *H. femorata.* These species are much larger than ground wētā, however, and the appearance of each type of plant in the faeces was noted in preliminary laboratory experiments, making identification easier.

differences between the sexes, but while nymphs younger than fifth instar ate less than 10% animal matter, older ones ate anything up to 100%.

A recent crop content analysis was that of a sample of the New Zealand mole cricket *Triamescaptor aotea*, a rare endemic burrowing insect (Orthoptera: Gryllotalpidae). This was the only study in which comparisons of crop "fullness" between different groups was attempted. Gutterson (1988) found that *T. aotea* crops were fuller in winter than other months, probably caused by a lower metabolic (and therefore digestion) rate due to the cold. He also noted that *T. aotea* fed only in moist conditions. Other results showed that this animal was omnivorous, with about half the overall diet comprising plant material and a quarter animal parts, the remainder being unidentified detritus. He attempted comparisons of crop components between several sub-samples. Different aged groups showed no significant differences in diet. Females appeared to eat more than males overall, and more cuticle of their own species (probably attributable to their consumption of first instar nymphs' exuviae whilst brooding them). Invertebrates were eaten more at times of the year when sampling indicated higher numbers being present (late spring - summer), suggesting that *T. aotea* is an opportunist feeder. Finally, more plant material was eaten by specimens sampled from moist habitats, though no explanation for this was offered.

The aim of this section of the study was to investigate the diet of *Hemiandrus* new sp. using a crop content analysis. The crop contents and crop fullness of wētā of different sexes, developmental stages and from different seasons were compared.

Methods.

All specimens used for this analysis were caught in "kill" pitfall traps as described in chapter 3. The crop, located anterior to the proventriculus in the thoracic region, was dissected from each wētā using fine tweezers under a dissecting microscope. The crop membrane was cut and any contents spread evenly over a slide to the size of a coverslip, with care being taken to remove any broken membrane and fat. Slides were air dried for a few minutes, and several drops of Lactophenol PVA containing the stain Lignin Pink were added to each. The mountant spread by the weight of the coverslip. As Lactophenol PVA shrinks considerably while drying, causing distortion of the slides' contents, all drying was at room temperature to minimise the effect, and samples were checked regularly. More mountant was added under the coverslip when necessary.

When dry (after two to three weeks), the slides were examined under a compound stereoscopic microscope at 160 x magnification. The important categories of material present were:

1. plant (including wood, leaf and stem)
2. animal (including chitin)
3. sand and other inorganic detritus
4. fungal spores

Material not identifiable as one of these categories was uncommon and ignored.

For the purposes of this analysis, each sex was divided into four size classes. The size classes did not represent instar groupings, but it was considered that significant differences in diet between different developmental stages would show in these groups. Size class limits and the number of dissected wētā of each class are shown in table 5.1.

Table 5.1. Size class limits (hind femur length) and the numbers (n) of each class dissected for the crop content analysis.

Wētā size class →		1	2	3	4
♀	size (mm)	< 4.7	4.7 - 7.0	7.1 - 9.4	> 9.4
	n	20	20	18	23
♂	size (mm)	< 4.7	4.7 - 6.7	6.8 - 8.9	> 8.9
	n	21	18	18	22

Totals of 81 female and 79 male wētā were dissected and examined.

For the eight classes of wētā, the percentage of individuals containing each food type was calculated. Measures of percentage occurrence do not take into account how much of a particular food category was eaten, but only what proportion of individuals in the sample the category occurred in.

To indicate the relative amounts of plant, animal and detritus eaten by *Hemiandrus* new sp., the percentages of each food category in each specimen was estimated. A coverslip-sized grid of 100 two millimetre squares (a randomly selected ten of which were darkened) was placed under each slide. The percentage of each kind of material present over each of the darkened squares was estimated by eye, averaged, and recorded as that individual wētā's crop content. Fungal spores were not measured in this way, due to their very small size (0.01 - 0.08mm diameter) and the fact that quite large numbers covered very small areas of the slides. Instead the number of spores per darkened square was counted.

The mean percentages of the major food type present (plant) was compared between the sexes and the size classes.

Before each crop was slit open, its fullness was estimated by eye, and scored from 0 (empty) to 3 (distended). Crop fullness was compared between the sexes, developmental stages and seasons.

Any identifiable invertebrates found in crops were recorded.

Results.

Figure 5.1a shows the percentages of each female size class in which the four food categories were present. Figure 5.1b shows the percentages of each male size class in which the four food categories were present. For example, 18 of the 20 specimens (=90%) of *female size class 1* had plant material in their crops (fig. 5.1a). Most of this size class (80%) also had some animal material and a few some detritus and fungal spores, so the percentages for each size class add up to more than 100%. Wētā in which the crop was empty are excluded from these figures.

Plant material (including wood, stem and leaf) was present most frequently, being found in 76 - 90% of specimens in these sub-samples. Animal material (mainly arthropod exoskeleton and shredded muscle tissue) was present in 50 - 88% of specimens. Inorganic detritus (mainly fine sand or silt) was present in 22 - 81% of specimens. Twelve percent of all (pooled) crops contained only plant matter, while 18% contained only animal remains.

Fungal spores were present in 11 - 44% of crops, but were very abundant in some individuals. The smallest of the spores numbered many thousands in a few crops. These spores were probably from cellulose degrading moulds in the Deuteromycetes (W. Gill, pers. comm). Other spores present in smaller numbers were some from a leaf parasite, possibly *Chaetomium* sp. (order: Sordariales) and those of several types of mushroom (W. Gill, pers. comm).

Minute transparent stellate leaf hairs (diameter 0.5mm) were present in variable numbers in many wētā crops (W. Gill, pers. comm.).

The mean percentages of plant material eaten by female and male wētā were compared using the *t*-test for differences between means (Ott and Mendenhall, 1985). Females contained a mean of 64.0% plant material and males 56.5%. As the 95% confidence interval for the difference between the means contained zero (L_{lower} = -3.8%, L_{upper} = 18.6%), indicating that the difference between the means may be zero, there were no significant differences between the percentages of plant material eaten by female and male wētā (α = 0.05).

Figure 5.2 shows the mean percentages of plant, animal and detrital material eaten by each size class of female and male wētā, with 95% confidence intervals. Variation was large, and as all confidence intervals for each category overlap, diets of the four wētā classes showed no significant differences (Sokal and Rohlf, 1981). Overall (all groups pooled), plant material comprised 60% of the crop contents, animal 34% and detritus 6%.

Figure 5.2 suggests that both females and males of size class 2 eat a smaller percentage of plant material than most other classes. This size class (which approximately coincides with instars four and five for both sexes) was present in spring and autumn but rarely in summer (figs. 4.4a and 4.4b). To test the hypotheses that wētā were eating more plant material in summer than the other seasons,

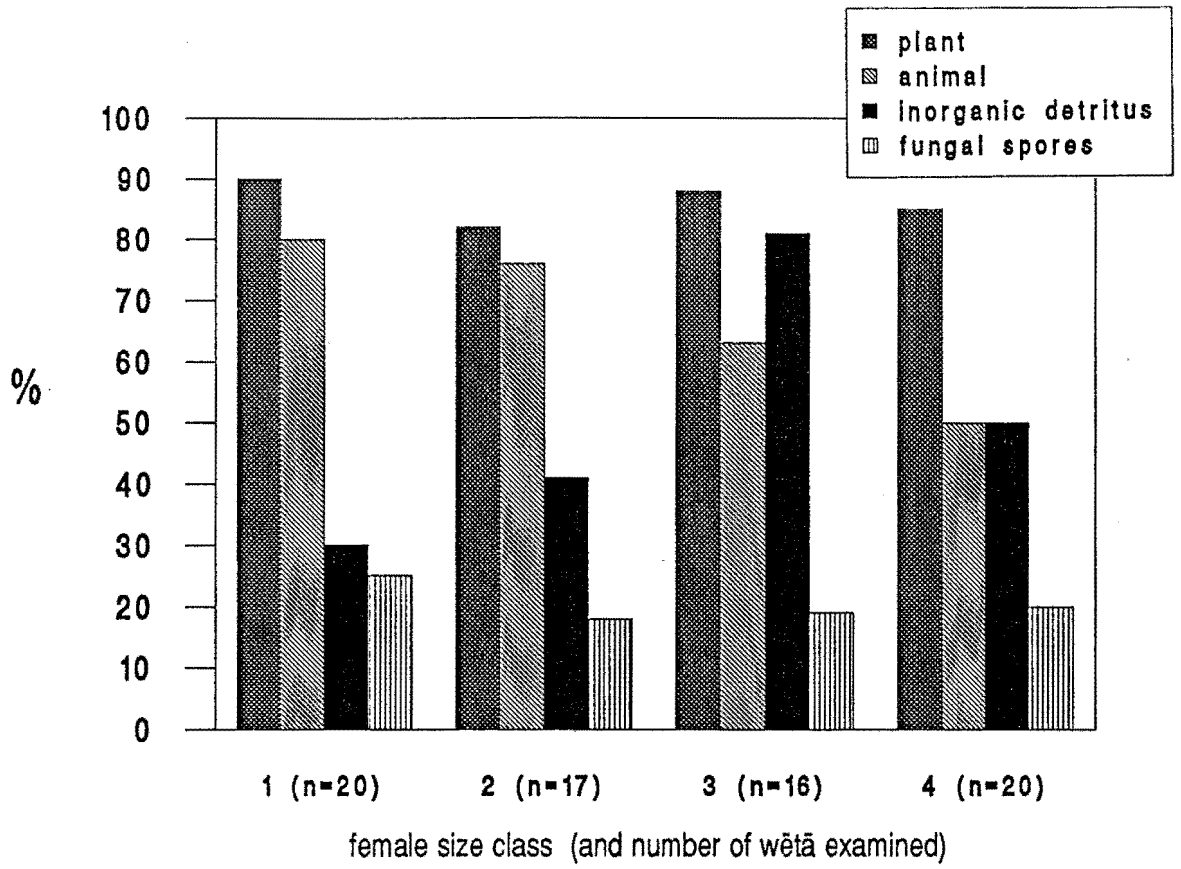

Figure 5.1a. Percentage occurrences of food categories in female *Hemiandrus* new sp.

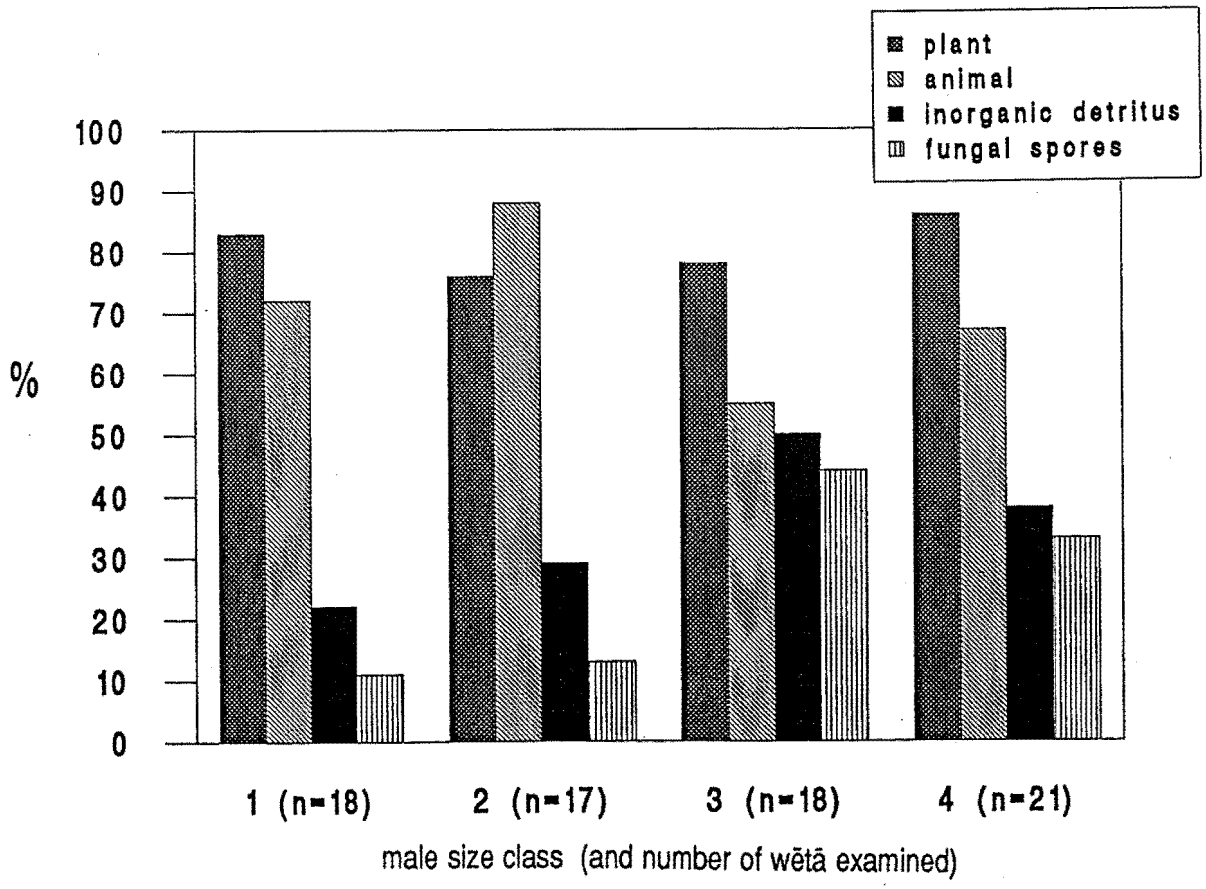

Figure 5.1b. Percentage occurrences of food categories in male *Hemiandrus* new sp.

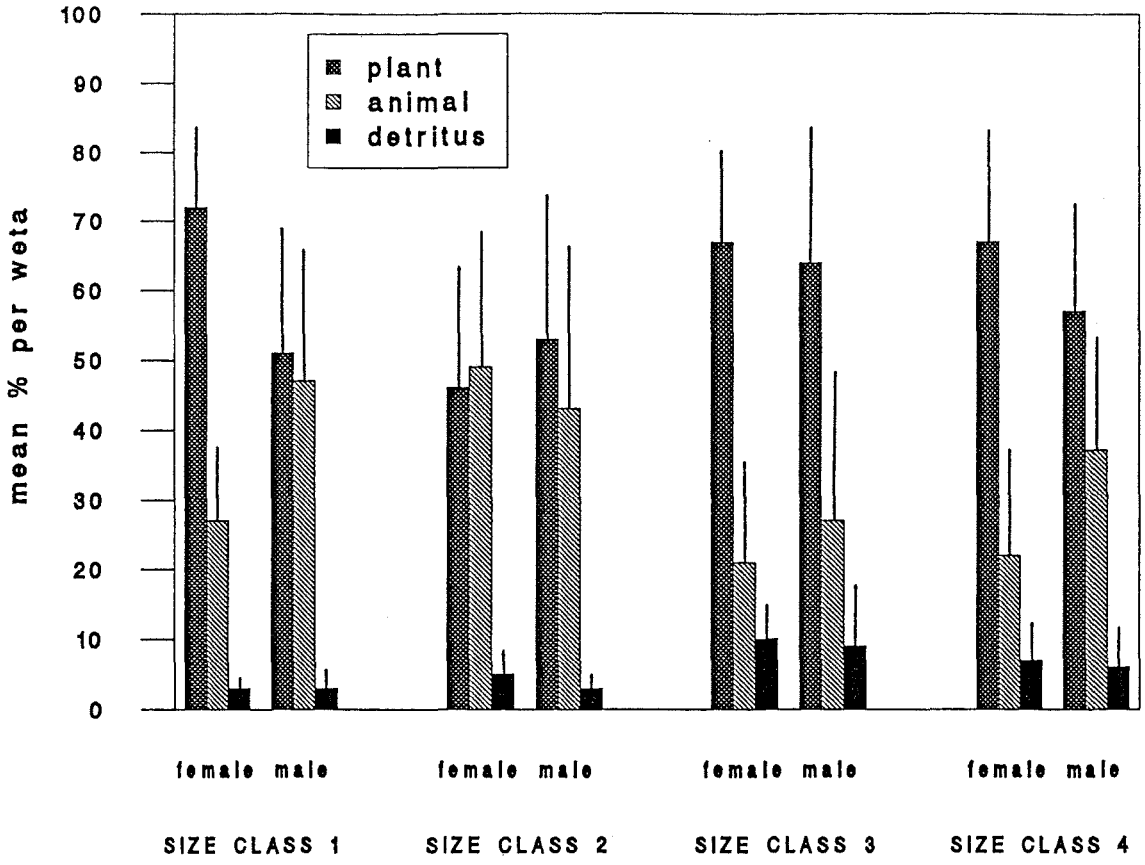

Figure 5.2. Mean percentages of plant, animal and detrital material eaten by each class of wētā, with 95% confidence intervals.

the data from summer (December, January and February) specimens (excluding those with empty crops) were pooled as were the data from all other specimens. The crops of wētā trapped in summer contained a mean of 66.5% plant material, while those from the other seasons contained 51.6% (fig. 5.3). These values were compared using the *t*-test for differences between means (Ott and Mendenhall, 1985). As the 98% confidence interval for the difference between the two means did not contain zero (L_{lower} = 0.7%, L_{upper} = 29.1%), summer wētā eat a significantly greater proportion of plant matter than those from other seasons (α = 0.02).

The dependence of crop fullness on wētā size class with sexes pooled, wētā sex, and season of capture were tested using the Chi-squared test of independence. Data are presented in table 5.2. Crop fullness was not dependent on size class with sexes pooled (critical $\chi^2_{(d.f.=9,\ \alpha=0.05)}$ = 16.9; calculated χ^2 = 3.42); sex (critical $\chi^2_{(d.f.=3,\ \alpha=0.05)}$ = 7.82; calculated χ^2 = 1.31); or season of capture (critical $\chi^2_{(d.f.=3,\ \alpha=0.05)}$ = 7.82; calculated χ^2 =3.56).

Table 5.2. Crop fullness data from the 160 *Hemiandrus* new sp. dissected. Values represent the frequencies of each level of fullness.

crop fullness ↓	wētā size class (sexes pooled)				♀	♂	summer	other seasons	totals
	1	2	3	4					
0	3	4	1	5	8	5	7	6	13
1	22	22	21	24	46	43	69	20	89
2	11	7	10	13	20	21	32	9	41
3	5	4	3	5	7	10	13	4	17
totals	41	37	35	47	81	79	121	39	160

A few prey invertebrates were identifiable to the taxonomic level of family or lower. The commonest of these was a small collembolan (Arthropleona: Poduroidea) present in large numbers in some crops. Another frequently found invertebrate was the weevil *Otiorynchus ovatus* (Coleoptera: Curculionidae). A small bug of the family Lygaeidae (Insecta, Hemiptera) was found whole in one crop. Fragments of flies (Diptera) and aphids (Hemiptera) were also noted.

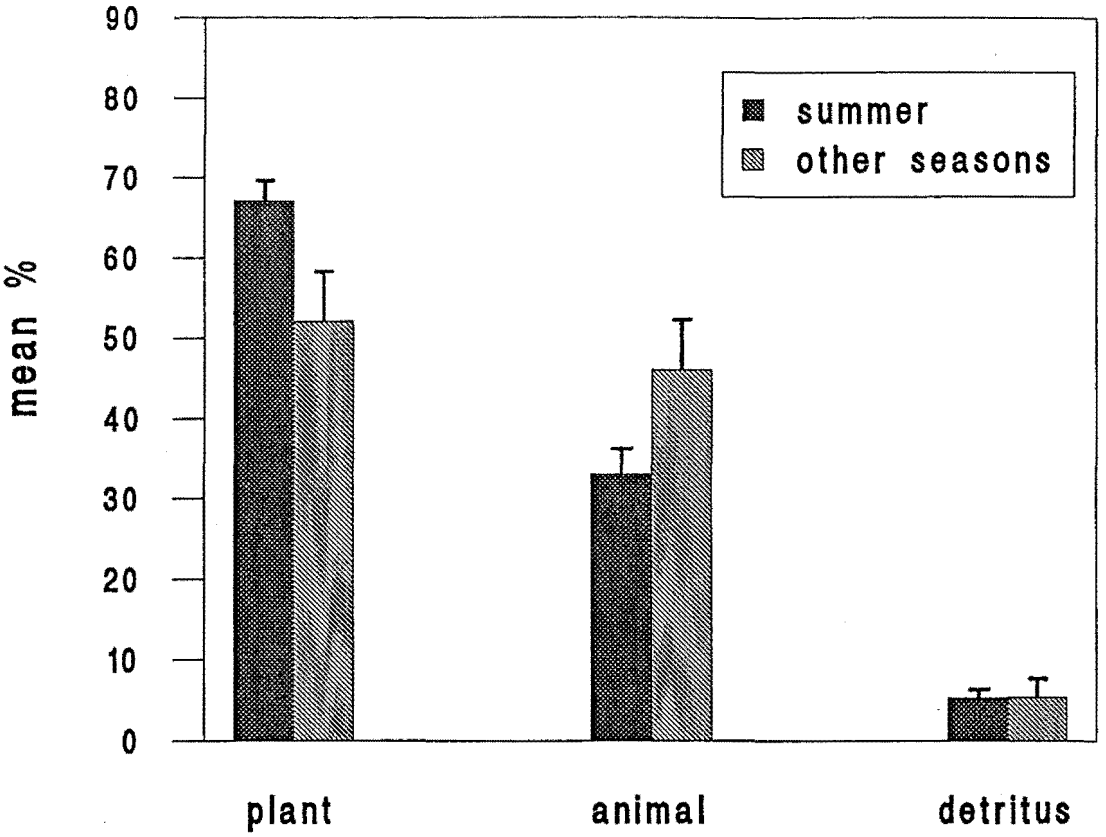

Figure 5.3. Mean percentages (± S.E.) of plant, animal and detrital material eaten by wētā captured during summer (December, January and February), and those eaten by wētā captured in the other seasons (pooled).

Discussion.

Hemiandrus new sp. is an omnivore with both plant and animal material found in most crops examined. It seems that the species does not have highly specific feeding requirements as it successfully inhabits areas in which plant communities have been extensively modified from their original condition (i.e. native tussock grasslands have been largely replaced by adventive weed associations).

Plant matter was nearly twice as abundant in crops as animal matter overall, but 18% of all specimens examined contained entirely animal matter while only 12% contained entirely plant matter. This suggests that *Hemiandrus* new sp. may have a preference for animal food. Laboratory observations of feeding support this suggestion. Other wētā species known to be generally herbivorous or omnivorous have shown a preference for animal food in the laboratory (e.g. *Deinacrida rugosa* (Ramsay, 1955), *Hemideina femorata* and *H. maori* (Little, 1980)).

It is probable that most omnivorous species will take animal food when available, due to its greater nutritional value. Therefore it seems likely that *Hemiandrus* new sp. eats plant material supplemented by any animal food available. Invertebrate food may be caught alive or scavenged. Further evidence that *Hemiandrus* new sp. takes animal prey opportunistically is provided by the large numbers of collembolans in the crops of a some individuals. Many of those crops with large numbers of Collembola were from wētā trapped on rainy nights. Collembola are soil living animals but congregate on the surface in very large numbers when rain water saturates the soil (Naumann, 1991), making them available to wētā.

Unlike other ground wētā in which diet has been studied (*Hemiandrus* sp. (Wahid, 1978); *Zealandosandrus gracilis* (Cary, 1981) and *Z. subantarcticus* (Butts, 1983)), *Hemiandrus* new sp. from Tekapo shows no differences in diet between sexes or developmental stages. However, in summer wētā eat significantly more plant material than in the other seasons. This is surprising considering that invertebrate food is likely to be more abundant (though not necessarily easier prey) in the warmer months of summer than colder months. Additionally adult female *Hemiandrus* new sp. oviposit in late summer, so presumably require extra nutrients (especially protein which can be most easily obtained from animal material (Little, 1980)) for ovarian development during early summer.

Several types of fungal spores were present in *Hemiandrus* new sp. crops, suggesting that they are eating decomposing organic matter. The presence of leaf parasite spores and stellate leaf hairs suggest that *Hemiandrus* new sp. is eating living leaves, but no plant species were identified from the crops. Likewise, the presence of cellulose degrading mould spores in crops indicates some consumption of dead woody material.

Collembolans may be opportunistically taken when abundant, but other larger prey invertebrates are frequently eaten. Most of the food category "animal" consisted of pieces of arthropod cuticle not

identified to any lower taxonomic level. Clearly some larger prey such as beetles are eaten, but it is unknown whether they are usually captured of scavenged. Other *Hemiandrus* species are generally predators (Cary, 1981; Butts, 1983) so it is likely that the present species is also. Ground wētā from wet forest habitats (e.g. *Zealandosandrus gracilis* and *Z. subantarcticus*) are predominantly or entirely carnivorous. This may be because of the abundance of invertebrate prey readily available in forest leaf litter. Wētā from arid regions lacking in leaf litter will not have access to so much animal material.

Inorganic detritus was present in small amounts in all groups of wētā. This material (mainly sand and silt) was probably accidentally ingested as the wētā fed, or perhaps swallowed as the wētā constructed their burrows.

Chapter 6
Burrowing and Burrow Structure

Introduction.

Ground wētā spend much of their lives in burrows. For this reason the structure of burrows and the burrowing behaviour of *Hemiandrus* new sp. was investigated. Little information is available on ground wētā burrowing in New Zealand. It has however, been noted that those species with short ovipositors (*Hemiandrus* spp.) tend to oviposit inside their burrows (P. Barrett, pers. comm.) and those with longer ones (*Zealandosandrus* spp.) penetrate the soil surface from above (Wahid, 1978; Cary, 1981). It appears that the depth to which these longer ovipositors can reach is sufficient to provide suitable conditions for incubation of the eggs. Ground wētā from arid regions may be more likely to oviposit in their burrows to prevent the eggs experiencing temperature extremes and very low humidity closer to the surface.

Crickets of the Australian genus *Bothriogryllacris* (Orthoptera: Gryllacrididae) burrow in the soils of arid regions. To avoid desiccation, these species line their burrows with "silk" and cap the entrance with sand grains or a stone (Naumann, 1991). A similar technique appears to be employed by some of New Zealand's ground wētā. Some species from arid regions (e.g. *H. focalis* from the mountains of central Otago and *Hemiandrus* new sp. from Tekapo) form caps from soil and sand to close the burrow (fig. 6.1). Caps are barely visible on the soil surface (fig. 6.2). It is possible that some species of ground wētā from humid habitats line the inside surfaces of their burrows to keep moisture out (P. Barrett, pers. comm.).

Hemiandrus pallitarsis from the Wellington region was previously the only species of ground wētā for which detailed observations of burrowing have been recorded. The following account is from Paul Barrett of the Wellington Zoological Gardens. *Hemiandrus pallitarsis* lives in forest or grassland habitats, and its burrows are found in well drained, often raised places to avoid being flooded out. Wētā burrows may be very close to each other. Their inhabitants will be aware of the presence of neighbours, but defensive of their own burrows. Although *H. pallitarsis* are capable of making their own burrows, they may use and extend existing tunnels made by exiting porina (Lepidoptera: Hepialidae) pupae or other large moths. *H. pallitarsis* constructs a bent foot at the base of the burrow, perhaps to escape the probings of kiwi. Mating may take place inside the female's burrow or on the ground surface outside, and the female oviposits in the burrow's foot, which it enlarges for the purpose. Hatchling wētā stay in the female's burrow until the end of the first instar, but probably do not return once they have left.

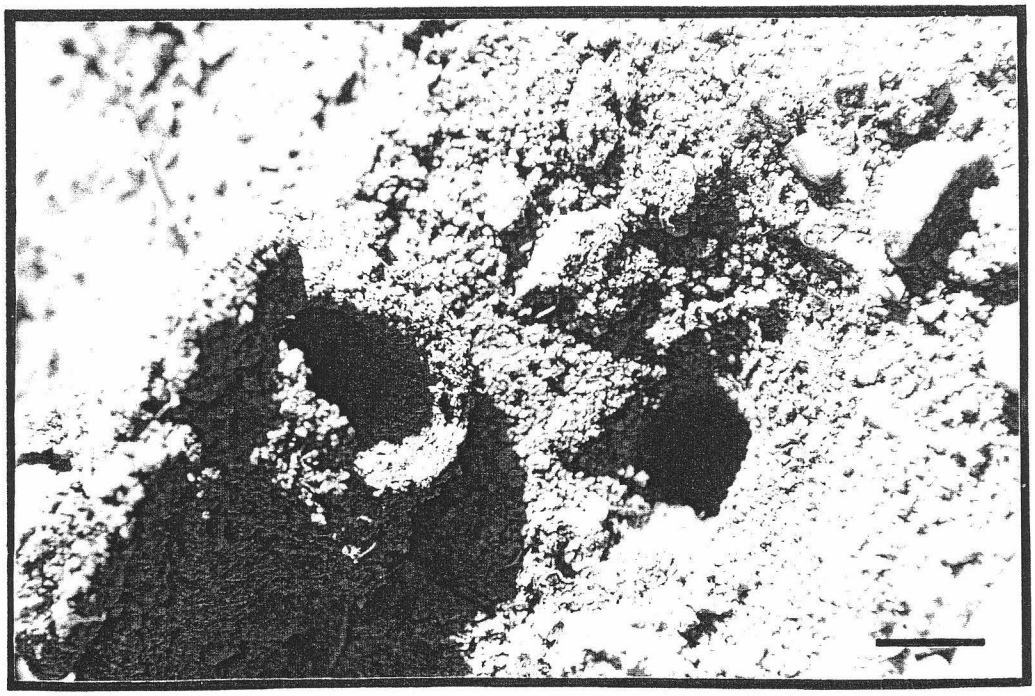

Figure 6.1. *Hemiandrus* new sp. burrow entrance with cap removed. Scale bar = 10mm.

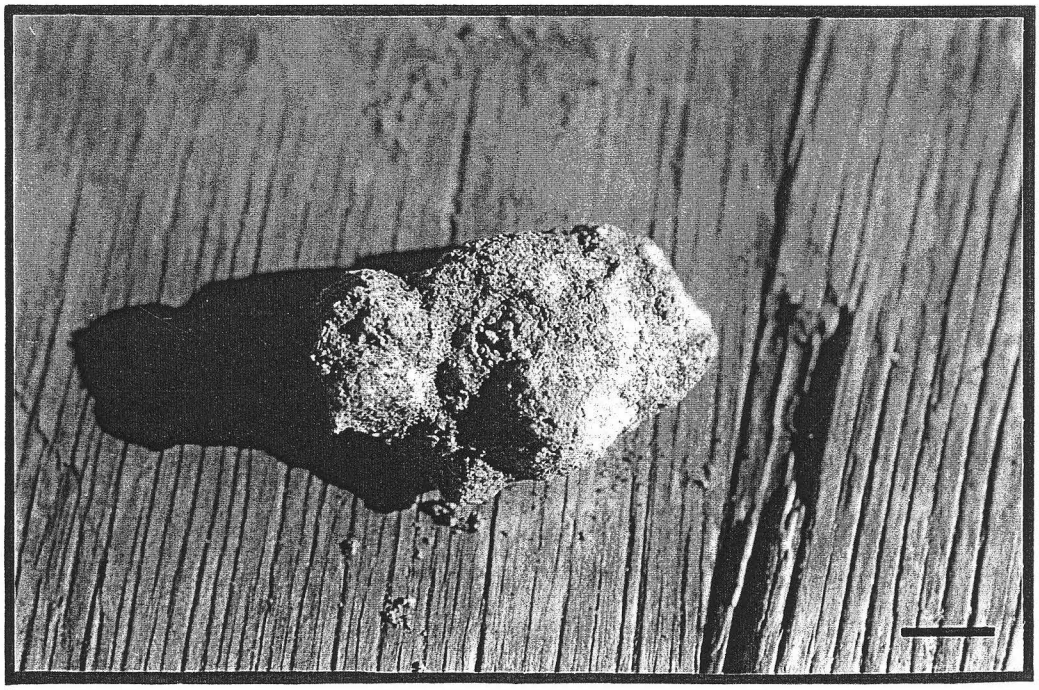

Figure 6.2. "Frost-heaved" soil with circular burrow cap of *Hemiandrus* new sp. in the centre. Scale bar = 10mm.

Methods.

1. Laboratory observations.

Burrowing behaviour was observed in a 0.6m x 0.9m observation cage during darkness with the aid of a dim red light (lighting is described in appendix 2). Differences between adult male and female burrowing were noted, as were those between juveniles and adults.

2. Burrow structure in the field.

Casts were made of wētā burrows found from November 1994 to January 1995. The burrow entrances were usually sealed and invisible, but could be found by breaking off small raised pieces of "frost-heaved" soil common on the river terraces. Burrows were not found in very stony or gravelly areas.

Initially a molten wax casting method, as described by Gutterson (1988) for burrows of the New Zealand mole cricket *Triamescaptor aotea*, was attempted, but this proved time consuming and the casts were brittle and incomplete. "Vinamold", a soft re-heatable synthetic rubber casting material was also trialed, but required such high temperatures to become sufficiently liquid that it was impractical and dangerous in the field.

Plaster of paris was poured down each burrow and left for at least one hour to set before excavation of the resultant cast. The solution shrinks considerably during setting (as water is absorbed into the walls of the burrow), so continuous topping up was necessary, making the process very time consuming. Casts were carefully dug out of the substrate but proved quite brittle and often broke. Successfully excavated casts were stored in 70% alcohol to preserve the contents. After cleaning, measuring and photographing, the casts were broken apart to reveal the sex and developmental stage of the resident wētā.

Results.

1. Laboratory observations.

Experimental wētā housed individually in one litre plastic pottles often made short burrows with a closed cap. The cap was formed on the top of a pile of soil removed during excavation of the burrow, and resembled those found in the field (fig. 6.1).

Basic burrowing technique: The wētā anchors itself by all six legs. Soil is scooped under the head and pushed back both by the pivoting of the head and the rearward movement of the whole animal. The fore and hind legs help to position the pile of loose soil. After several "scoops" of soil are collected under the abdomen, the pile is flicked out the back by two or more swift alternate kicks of the hind legs. Large pieces of sand, stones and debris (up to about the size of the wētā's head) are removed individually with the mandibles. Pieces larger than this are left and the burrow diverted around them.

No differences were observed between the burrowing behaviours of adult males and females, though adult wētā of both sexes tended to kick the soil away less frequently than juveniles, preferring to scoop it further backwards.

2. Burrow structure in the field.

Seventeen plaster of paris casts of wētā burrows were made, but seven of these were irreparably damaged during excavation. The remaining 10 varied in size and shape (figs. 6.2a - 6.2f). All burrows had a cap on them similar to that in figure 6.1, and consisted of a shaft terminating in a bulb of variable size. The inside surfaces of burrows were smooth and the constituent particles appeared to be cemented together (fig. 6.3). Burrows ranged in length from 90 - 155mm and all ended at or before the depth of substrate where the friable sand or soil overlay coarser stones and rocks. No more than one wētā was found in each burrow.

In December 1994 seven burrows were found on a 30° slope within an area of 0.15 m^2. All wētā were recovered, but only five of the casts were successfully excavated. The seven wētā were all female (two 5^{th} instar, three 6^{th} instar, one 8^{th} instar and one adult).

Three of the 5^{th}-6^{th} instar females' burrows were similar, being straight with a slightly enlarged bulb at the end (similar to that in figure 6.4a), while the other was shorter, wider and curved along its whole length (fig. 6.4b). The adult female had four partially developed eggs in its abdomen. Its burrow terminated in a very large bulb (35mm in diameter) (fig. 6.4c). The shafts of the burrows pointed straight down or towards the bank. One of the 5^{th} instar female wētā was in the process of ecdysis when the cast was made[15].

In the centre of this group of burrows and less than 10cm from one of them, the burrow of a large trapdoor spider was found.

The other five successfully excavated casts were taken from a flat area of about 1.5 m^2. Two of the burrows (those of one 7^{th} instar male and one 7^{th} instar female) had dimensions similar to the 5^{th} - 6^{th} instar females' described above (fig. 6.4a). The burrow of a 9^{th} instar male had a bulb running horizontally along the top of a layer of stones underlying the burrowable soil (fig. 6.4d).

The only cast made from an adult male's burrow was unlike any other in having two shafts (fig. 6.4e). The wētā was dead in its burrow before casting and was partially decomposed. Several maggots of a small fly were found amongst its remains. An adult female's burrow found in the same area had an enlarged bulb (21mm in diameter) curved nearly horizontal. In this burrow 36 eggs were found with the wētā (fig. 6.4f).

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[15]Three captive wētā were observed during ecdysis while in their burrows.

Figure 6.3. *Hemiandrus* new sp. burrow excavated *in-situ*. Note the curve at the lower end. Scale bar = 10mm.

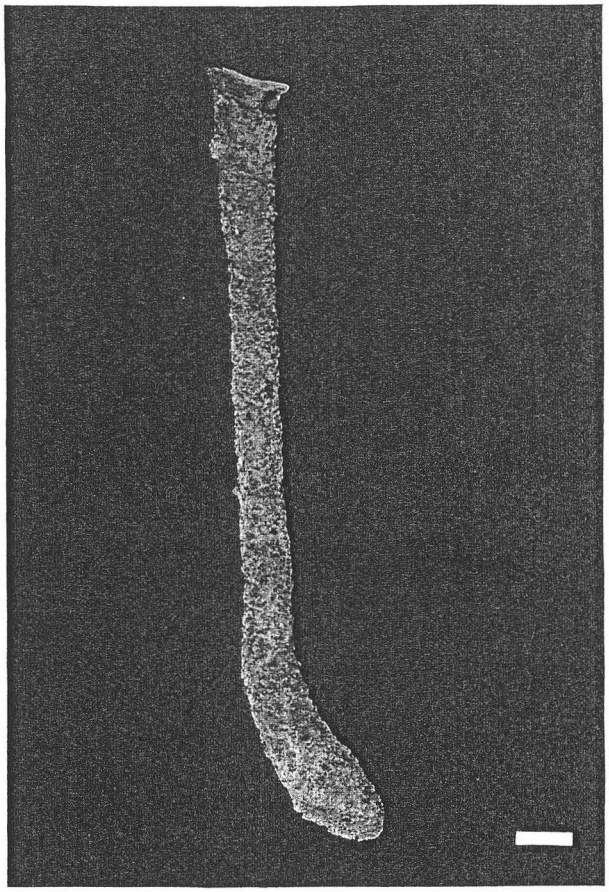

Figure 6.4a. Typical cast taken from a 5th - 6th instar *Hemiandrus* new sp. burrow. Scale bar = 10mm.

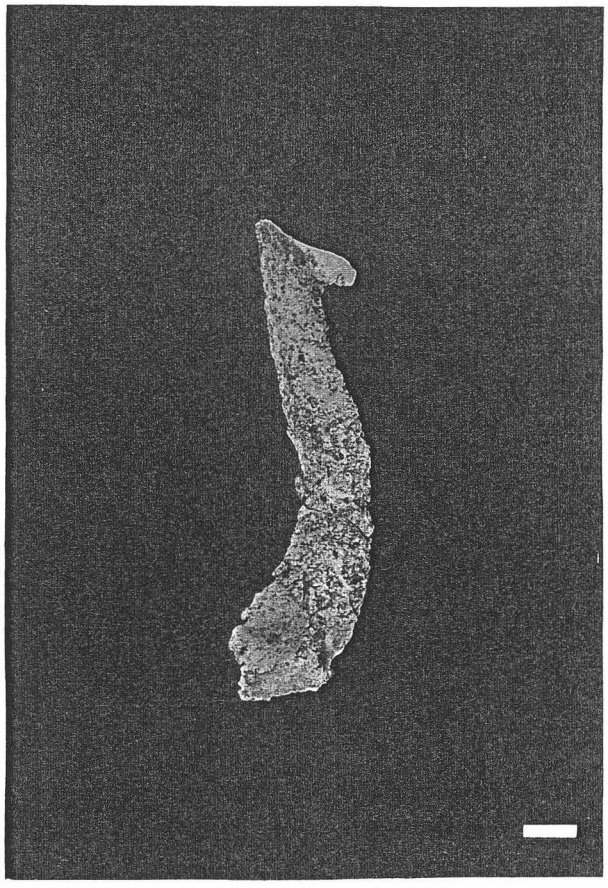

Figure 6.4b. Cast of a 5th instar female *Hemiandrus* new sp. burrow. Scale bar = 10mm.

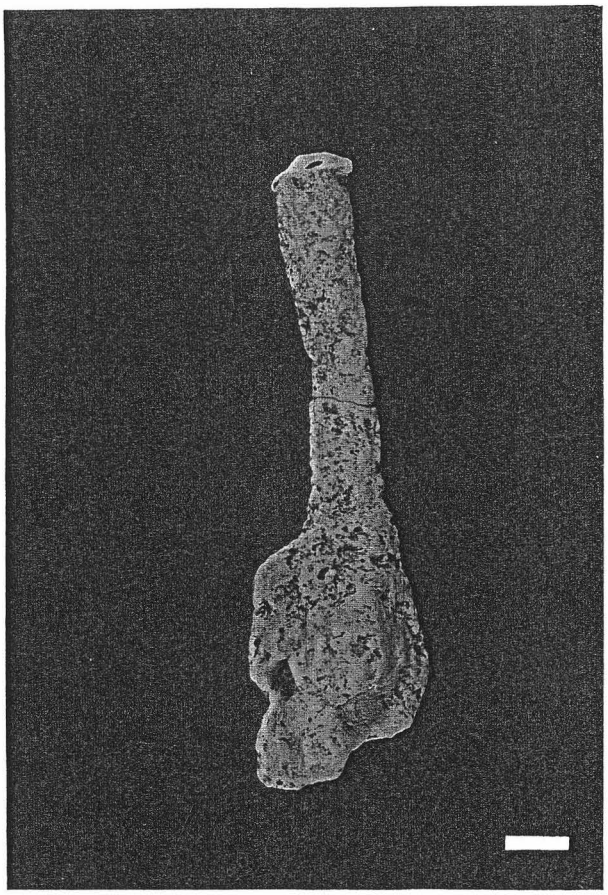

Figure 6.4c. Cast of an adult female *Hemiandrus* new sp. burrow. Scale bar = 10mm.

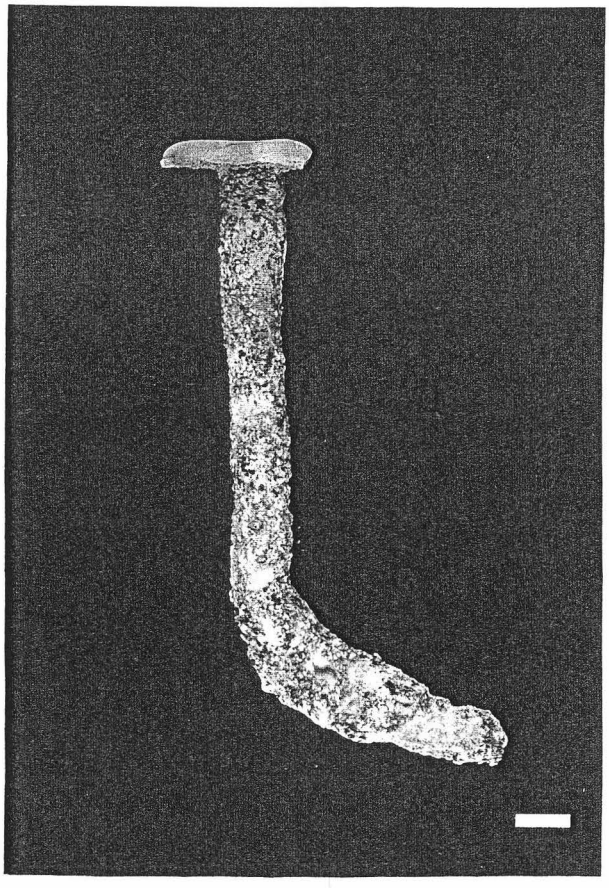

Figure 6.4d. Cast of a 9th instar male *Hemiandrus* new sp. burrow, with a nearly horizontal bulb. Scale bar = 10mm.

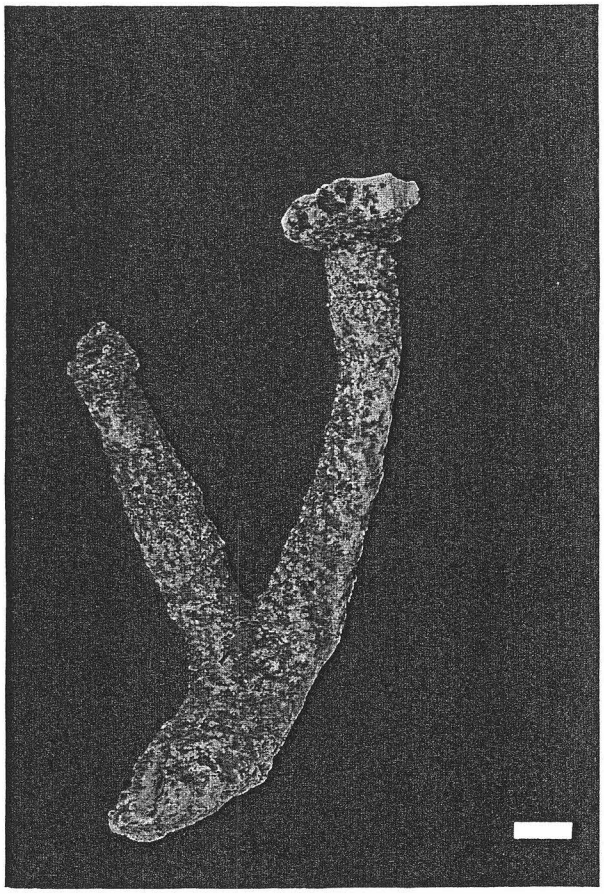

Figure 6.4e. Cast of an adult male *Hemiandrus* new sp. burrow, with two shafts. Scale bar = 10mm.

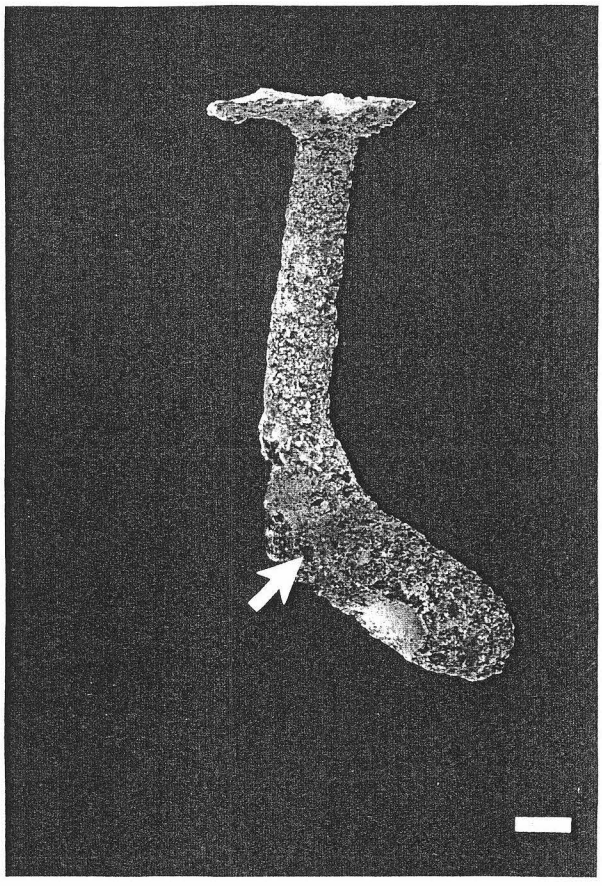

Figure 6.4f. Cast of an adult female *Hemiandrus* new sp. burrow, with an enlarged chamber and some eggs visible (arrow). Scale bar = 10mm.

Discussion.

Despite the small number of *Hemiandrus* new sp. burrows cast, it appears that the structure of burrows follows a regular pattern, and is similar to that described for *Hemiandrus pallitarsis* (P. Barrett, pers. comm.). Burrows consist of a straight main shaft, usually vertical or nearly so, terminating in an enlarged chamber or bulb. Bulbs are often curved horizontally or nearly so along the top of underlying rocks (fig. 6.5). Burrows seldom penetrate far into the underlying layer and the presence of burrows may be dependent to a large extent on the existence of suitable friable substrate. Generally, burrows are sealed with a cap, perhaps for protection from predators or parasites, or to minimise desiccation. The inside surface of burrows is smooth and may be strengthened with some sort of cement secreted by the wētā. It is unknown whether *Hemiandrus* new sp. use exit holes of porina moth pupae as burrows, but this group of moths was uncommon in the region. However, the burrows of several other abundant invertebrates such as trapdoor spiders (*Cantauria* spp.) and tiger beetles (*Neocicindela* spp.) may have been suitable.

The burrows of adult females possess an enlarged bulb, and oviposition occurs in this chamber. Unfortunately no evidence was found to clarify whether or not 1st instar nymphs remain in the female parent's burrow after hatching as happens in other species (e.g. *Hemiandrus* sp. from Banks Peninsula and *H. pallitarsis* from Wellington). As nymphs of this age were frequently caught in pitfall traps (chapter 4), they clearly are not confined to the burrow, but still may use it as a retreat instead of making their own.

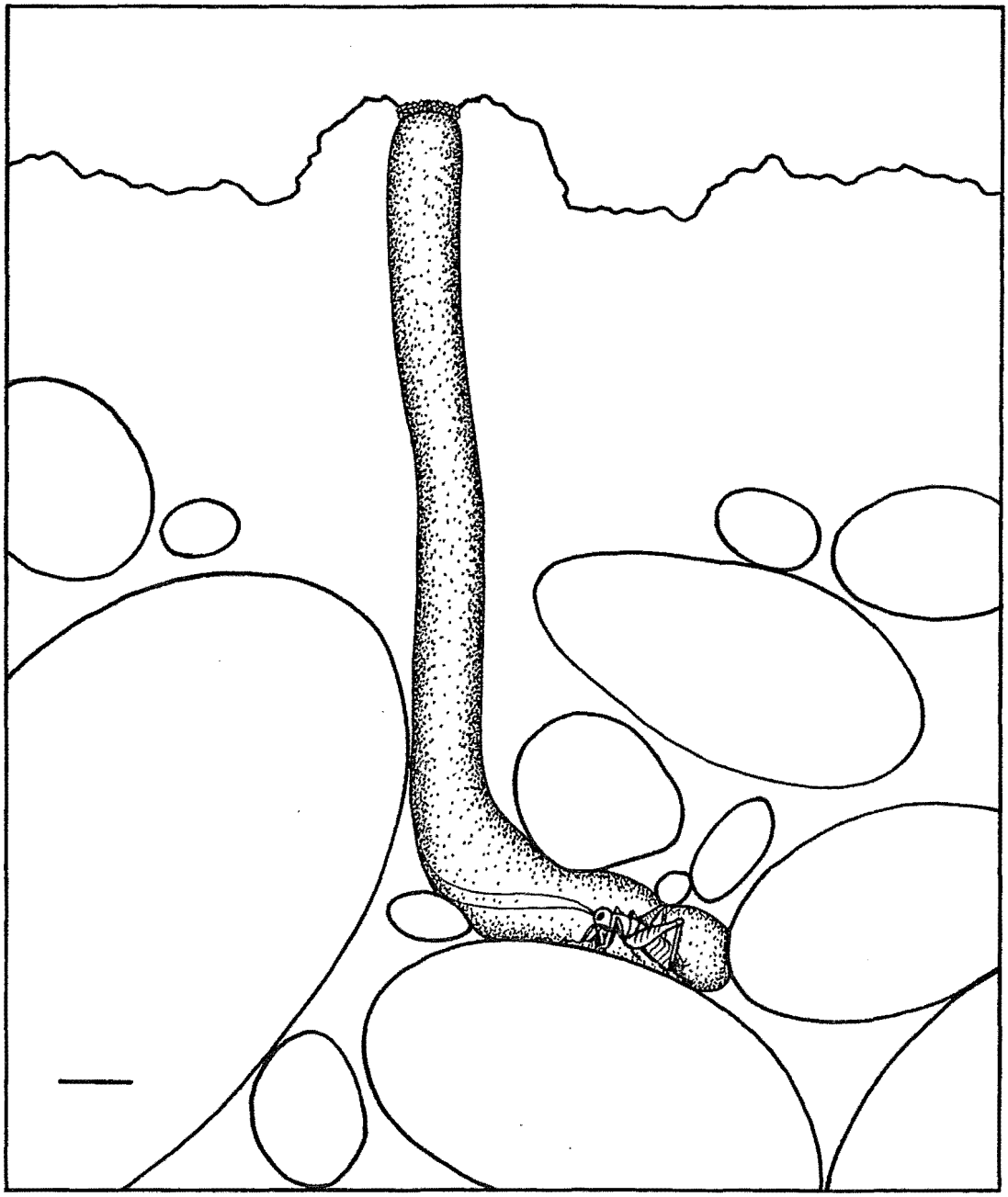

Figure 6.5. Stylised late instar *Hemiandrus* new sp. burrow, showing cap (top), shaft and terminal chamber among stones. Scale bar = 10mm.

Chapter 7
Parasites and Predators

A. Parasites.

Introduction.

Although parasitism has been recorded in New Zealand Anostostomatidae for over a century, very little work has been specifically devoted to this area of wētā biology. Dale (1967) described the new genus and species of nematode *Wetanema hula* after its discovery in the tree wētā *Hemideina thoracica*. He noted that the hosts of nematodes from this family (Thalostomatidae) are usually detritus feeders, a form of feeding present to a limited extent in tree wētā, implying that the parasite is transferred to the host from this source. Meads (1989a, 1990) reported large numbers of *Deinacrida parva* drowned in pools of the Hapuku and Kowhai Rivers of the Seaward Kaikoura Range, in association with a new species of wētā-specific gordian worm. The intermediate stage of the parasite is not known, but may be the larvae of an aquatic insect such as a damselfly (Odonata) (Meads, 1989a).

Observations of parasitic mites (Ramsay, 1975) and gregarines (Maskell, 1926; Dale, 1967) have been made in *Deinacrida* and *Hemideina* species, but only one study has focused on parasitism in a ground wētā species.

Cary (1981) reported external mites (not identified) on a very small proportion of the ground wētā *Zealandosandrus gracilis*. Dissections of anaesthetized animals revealed that about one in three harboured sporozoan parasites of the family Gregarinidae. The parasites were found in the midgut, and when large numbers were present, did have a noticeable effect on the health of the host. The dissected specimens had been held in the laboratory for some time, and under these sub-optimal conditions it is common for parasites to proliferate (Harry, 1967).

The purpose of this section was to determine whether parasitism was significantly affecting *Hemiandrus* new sp.

Methods.

All wētā collected during the study were examined under a dissecting microscope for the presence of external parasites. Live specimens were examined at the same time as they were measured to avoid subjecting them to an extra dose of CO_2 (see chapter 4).

Internal parasites were searched for by dissecting the gut and other abdominal tissues of four anaesthetized live and ten recently killed preserved specimens (adults or penultimate instars of both sexes) under a dissecting microscope.

Results and Discussion.

In total, 273 female and 224 male *Hemiandrus* new sp. were examined for external parasites, but no parasites were found. As the majority of these wētā were trapped in "kill" pitfall traps, it is possible that the preservative may have caused any external parasites (e.g. mites) to abandon the wētā's body and become lost amongst the small animals and detritus at the bottom of the trap. However, at least 176 of those wētā examined were freshly caught live specimens. It appears that this species does not harbour external parasites, or if it does, they are very rare.

No parasitic nematodes or any other internal parasites were found in the gut or abdominal tissues of the 14 *Hemiandrus* new sp. dissected. Three very small free-living soil nematodes were isolated from the gut of one of the preserved adult females. These were probably ingested with food (J. McKenzie, pers. comm.).

B. Predators.

Introduction.

It is known from many studies that in New Zealand, introduced predatory mammals eat native invertebrates. Feral cats (*Felis catus*) often eat invertebrates as an alternative to their usual diet of rodents and other small mammals. The giant wētā *Deinacrida carinata* was heavily preyed upon by cats on Herekopare Island (Foveaux Strait) prior to the eradication of the cats in 1970 (Fitzgerald and Veitch, 1985). In the Orongorongo Valley near Wellington, wētā were present in 75% of cat scats examined (Brockie, 1992).

In a study of the composition of cat scats found in the region of the present study, Ryan (1994) found invertebrates (mostly the Tekapo wētā *Hemiandrus* new sp.) in 43% of summer scats and 68% of autumn scats, though they were absent from those collected in winter[16]. Pierce (1987), also working alongside the Tekapo River, found that juvenile cats in summer and autumn preyed mainly on invertebrates and lizards, switching to rabbits as they matured. The finding that juveniles target smaller prey such as insects was confirmed by Pascoe (1995). However, even adult cats preyed on the tree wētā *Hemideina maori*. Its remains were present in 5 - 25% of scats all year round, indicating that this wētā is active throughout the winter. Pascoe (1995) found the remains of wētā (both *H. maori* and *Hemiandrus* new sp.) in the guts of 23% of cats from the Mackenzie Basin.

Like the cats in the Tekapo River region, ferrets (*Mustela furo*) eat mostly rabbits, but juveniles and females also take invertebrates and lizards. *Hemideina maori* appeared in 10% of adult female ferrets' scats (except in winter) and 20 - 25% of juveniles' scats (in autumn) (Pierce, 1987).

Rodents, especially rats, appear uncommon in the areas surrounding the Tekapo River. A. Pascoe (pers. comm.) trapped a few Norway rats (*Rattus norvegicus*) near waterways but recorded no footprints in numerous tracking tunnels. Pierce (1987) observed *R. norvegicus*, but caught none in 400 trap nights over late winter. Many studies have shown that rats are important predators of invertebrates. Arthropods, dominated by cave wētā, made up over half the volume of ship rats' (*R. rattus*) stomach contents in a study on Stewart Island (Gales, 1982). Daniel (1973) found that ship rats from the Orongorongo Valley ate tree wētā as their main food source in spring and summer.

Mice (*Mus musculus*) are also known to prey on invertebrates but are not usually common in the present study area (Pierce, 1987). There are no data available on the diets of mice from the Tekapo River region. In the Orongorongo forest, mice ate wētā, including ground wētā, all year round (Brockie, 1992). Badan (1986), comparing mouse diet in two types of forest in the North Island,

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[16]Predation of wētā during the winter seems unlikely due to very low or nil activity of these insects in cold conditions. Lab specimens were increasingly inactive below about 6°C, though would readily respond to disturbance. Below about 3°C all movement was lethargic.

found that 80 - 90% of stomachs (mostly in summer) contained adult arthropods.

Interestingly, Pierce (1987) considers that the lack of rodents in the Tekapo River area means that other predatory mammals (especially young cats and ferrets) turn to invertebrates and lizards as a substitute until they are large and skilled enough to catch rabbits.

Hedgehogs (*Erinaceus europaeus*) are insectivorous and certainly likely predators of the Tekapo wētā. They are surprisingly efficient hunters, and will generally eat most suitably sized animals they come across (Woods, 1970). Common foods in New Zealand pastures are grassgrubs, porina moth larvae (Campbell, 1973), slugs, worms and earwigs (Woods, 1970). Wētā (*Hemiandrus* sp.) remains were present but infrequent in one study of hedgehog gut contents (Woods, 1970). It is known that hedgehog populations comprise large numbers of nomadic individuals compared to those which hold territories. This means that any local reductions in hedgehog numbers will generally be countered by immigration from nearby (A. Pascoe, pers. comm.).

Little owls (*Athene noctua*) are present (personal observation) but their diet in the Mackenzie Basin has not been investigated. Marples (1942), in agreement with earlier English studies, found that in New Zealand this species is a ground feeder, taking invertebrates, especially caterpillars and beetles. Orthoptera (taxa not stated, but likely to be wētā as most other orthopterans are diurnal), were eaten in large numbers by a small proportion of owls. Small numbers of mice and lizards were also taken. Watt (1979), considered predation by little owls to be the most significant threat to the endangered flightless chafer beetle *Prodontria lewisi* from Cromwell.

Presently, the most significant native predators of the Tekapo wētā are probably other invertebrates. There are many predatory insects and arachnids of sufficient size to deal with this wētā. Trapdoor spiders (*Cantauria* spp.) and funnelweb spiders (*Porrhothele* spp. and *Hexathele* spp.) are all present and the trapdoor burrows are quite abundant. The burrow of a large trapdoor spider was found amongst a group of several wētā burrows and less than 10 centimetres from one of them (see chapter 6). Further possible invertebrate predators include the larvae of tiger beetles (*Neocicindela feredayi* and *N. dunedensis*) and carabid beetles (e.g. *Metaglymma* sp.).

The buff weka (*Gallirallus australis hectori*) has been extinct on mainland Canterbury since the 1920s[17] (O'Connor, 1976), but was formerly a likely wētā predator.

The only extant native vertebrates likely to prey upon nocturnal insects such as wētā are lizards. The common gecko *Hoplodactylus maculatus* is occasionally found throughout the study area (Pierce, 1987) and is primarily nocturnal (Tocher, 1992), though no specimens were examined. The other

[17]During the 1970s, the Wildlife Service unsuccessfully attempted to re-introduce buff weka from the Chatham Islands (then their sole refuge) to the Tekapo River area (N. Buttery, pers. comm.).

lizards present are very common diurnal skinks (*Leiolopisma* spp.) which are unlikely to eat nocturnal wētā.

The purpose of the present section was to identify which introduced mammals were the most important predators of *Hemiandrus* new sp.

Methods.

During the samples of January, February, October and November 1994, and January 1995, 20 break-back rat traps were set at site D (fig. 3.1), mostly close to pitfall traps but a few on the edges of the open area close to willow trees (*Salix* spp.). The traps were baited with bacon rind or salami and set for two or three nights.

During the samples of November and December 1993, and April, June and December 1994, 20 break-back mouse traps were similarly set and baited.

Hedgehog faeces were collected when found and examined for the presence of wētā remains.

Results.

No rats were trapped at site D in 240 trap nights. However, during the sample of June 1994, one Norway rat (*Rattus norvegicus*) was accidentally killed nearby. Examination of its gut contents showed no evidence of wētā remains.

Only three mice were trapped in the break-back traps in 280 trap nights over the study period, all during April 1994. Two other juvenile mice were accidentally trapped in "kill" pitfall traps set in the area of pine trees (fig. 3.1), also in April 1994. All of the mouse guts contained mainly plant material (possibly seeds) and no evidence of wētā remains was found.

One fresh road-killed hedgehog was collected in March 1994. In its stomach were the remains of several *Hemiandrus* new sp. One young hedgehog was accidentally killed in a rat trap in January 1995. Its gut contained at least five wētā. During December 1994 and January 1995 five samples of fresh hedgehog faeces were collected from open scrubby and grassy areas near site D. Wētā remains were present in four of them.

Discussion.

It is not surprising that rats were not trapped during the spring or summer since they are not common in the area, as indicated by previous work (Pierce, 1987). Additionally, during the warmer months natural foods are probably abundant making rats less tempted to take trap bait. The one Norway rat

caught was on a very cold night during the winter and its gut contents were mostly plant material, with no sign of wētā or any invertebrates. *Hemiandrus* new sp. are quiescent during the winter so are unlikely to be available as rat prey items then. There is evidence that feral cats in the area, which eat *Hemiandrus* new sp. during the summer and autumn, do not do so during the winter (Ryan, 1994). Where present, rats may prey on *Hemiandrus* new sp., as they are known insect predators, but considering their rarity in the present study area, are probably not significant.

Mice were more common than rats in the study area though their numbers may fluctuate considerably (A. Pascoe, pers. comm.). Although the sample size is very small, the present study provides no evidence that mice prey on the Tekapo wētā. The weather conditions during April 1994 (when all the mice were caught) were favourable for wētā activity as indicated by the number of wētā trapped during that sample, so presumably some wētā were available as prey. However, it is unlikely that *Hemiandrus* new sp. escapes predation from mice.

From the present evidence it appears that hedgehogs are the most important mammalian predators of the Tekapo wētā. They are found throughout the river terraces (A. Pascoe, pers. comm.) and are insectivorous. Cats, especially juveniles, may occasionally eat many wētā but hedgehogs seem to be consistently taking moderate numbers. Of 57 cat scats examined, Ryan (1994) found eight (=14%) with the remains of one or more *Hemiandrus* new sp., whereas of seven hedgehog guts or faeces examined in the present study, six (=85%) contained the wētā.

Little owls (*Athene noctua*) were present throughout the study area. However, if this owl preys on other potential predators of the Tekapo wētā (e.g. mice, geckoes and predatory invertebrates), as well as the wētā itself, its presence may not necessarily be a threat to the wētā population. The same may be true for cats and to a lesser extent hedgehogs, so further research may be required to clarify the predatory interactions between the species.

Chapter 8
Conservation of the Cromwell wētā

A. General Discussion.

The Threatened Wētā Recovery Plan (Rasch, 1992) summarised important steps required to devise conservation and management plans for threatened wētā species. Although at the time ground wētā were not considered, the process could be equally applied to them, or indeed almost any threatened insect.

The first step recommended was a review of the knowledge of the species, including an assessment of the following themes: taxonomic distinctiveness, abundance and distribution, habitat requirements, reproductive data, threats to the population and reasons for the decline.

The present study has attempted to assess many of the above topics for the Cromwell wētā (*Hemiandrus* sp.) from a study of an allopatric species, the closely related Tekapo wētā (*Hemiandrus* sp.). It may be acceptable to generalize among closely related species when considering habitat requirements, reproductive data and threats to the population. However, conclusions regarding taxonomy, abundance and distribution and reasons for the populations' decline can only come from a study of the Cromwell wētā itself.

Records of the Cromwell wētā (*Hemiandrus* sp.) are scarce but remnant populations may be widespread in Central Otago. The species is common on the Cromwell Chafer Reserve, and is extant as far away as Alexandra. The distribution is thought to be much reduced from previously, however, due to habitat loss from land development (e.g. forestry, orcharding, hydro-electric schemes), and degradation of remaining habitat by rabbits and weeds. The Cromwell Chafer Reserve is the only protected area where Cromwell wētā are known to exist in good numbers, and its original purpose as a reserve for the chafer beetle *Prodontria lewisi* provides an important precedent for conservation of threatened invertebrates. Recently the wētā has been found to exist in the Flat Top Hill Conservation Area, south-west of Alexandra. Current and future tenure review of pastoral leases in the Cromwell and Alexandra areas may lead to new reserves being established supporting remnant populations of the Cromwell wētā (B. McKinlay, pers. comm.). Continuing development of non-protected areas may eventually eliminate populations outside of reserves.

The Cromwell and Tekapo wētā species are morphologically similar. Male genitalia, usually invaluable for differentiating between species, are indistinguishable. However, significant differences in female genitalia, adult morphology and morphometrics confirm that the two taxa are distinct. Formal descriptions of the Cromwell and Tekapo *Hemiandrus* species are planned for 1995.

The Tekapo species is long-lived, taking over two years to mature (twice the life span of some giant wētā), and females require another year before ovipositing. Females lay a small number of large eggs in their burrows and tend the eggs and possibly early stage nymphs after hatching.

The Tekapo wētā is abundant in many areas. Indeed, almost all pitfall traps left long-term caught some wētā, suggesting that the population is almost continuous throughout those areas sampled. It is not restricted to the newer terraces close to rivers, and may be present in other parts of the Mackenzie Basin and beyond. As a close relative, the Cromwell wētā is likely to have similar habitat requirements to the Tekapo species, so should be able to thrive under suitable conditions. There are extensive river terraces along the Clutha and Manuherikia Rivers near Cromwell and the Clutha and Kawarau Rivers near Alexandra (though many hundreds of hectares of terrace were submerged by the filling of Lake Dunstan), the less disturbed or developed of which may support populations of Cromwell wētā. It appears, however, that many of the areas that Cromwell wētā were recorded from in the 1970s are no longer suitable habitat. If the extent of remnant populations of the Cromwell wētā were sought, extensive investigative sampling (preferably live pitfall trapping) around sites of past records should be a priority. The presence and distribution of the species over the remaining relatively undisturbed river terraces in the Cromwell and Alexandra areas should also be assessed.

It is clear that the most important environmental characteristic determining the distribution of the Tekapo wētā is the availability of fine "burrowable" silty soil. Ground wētā spend the majority of their lives, oviposit, and possibly rear their young in their burrows. Additionally, burrows provide shelter from predation, freezing and desiccation. Soils in the Cromwell region are subject to similar wind erosion problems as those of the Mackenzie Basin. Wind erosion is facilitated by plant depletion from severe overgrazing by rabbits and stock, coupled with frequent strong and dry winds, especially in summer. Maintenance and replenishment of natural vegetation communities to increase soil binding should be a priority wherever substantial populations of the Cromwell wētā are identified. Reestablishment of native plant species, for example tussocks, where these are disappearing should proceed in conjunction with rabbit control in these areas. Where appropriate, the removal of sheep and other stock would be advantageous, as would the cessation of fires, herbicide spraying, motorcycling, or any other activities which could lead to vegetation depletion and/or soil loss.

Tekapo wētā were rarely caught close to the Haldon camping ground (popular in the summer with anglers, boaters and rabbit shooters), and their abundance generally increased with distance from the camp. It is possible that the increased disturbance of soils nearer the camp by anglers' and shooters' vehicles and recreational motorcycles discourage wētā.

Although the density of Tekapo wētā in a pine plantation was greater than that in nearby areas, this was probably because the area the Ministry of Works selected for maximum tree growth coincided

with favourable wētā habitat (i.e. deep soils). An attractive but less likely hypothesis for the difference in wētā abundance is that wētā thrive in the returned "forest" environment because it is similar to the original dry podocarp - broadleaf forest of the region. If this was the case then the same hypothesis could be applied to the Cromwell wētā, as its present lowland habitat was, in pre-human times, similarly forested. The pine canopy at the study site was very open, however, and it is difficult to believe that conditions under it would be significantly different from those under the widespread large scrub plants. Even if the presence of plantation trees does not disadvantage wētā populations, gross land disturbance when the trees are felled would be very destructive to the habitat. The fact that wētā seem to survive so well under the trees may warrant further investigation.

Unlike other ground wētā investigated in New Zealand, *Hemiandrus* new sp. from Tekapo is a predominantly herbivorous omnivore. It is probable that the Cromwell wētā, being from a similar habitat and climate, shows a comparable diet. The distributions and abundances of either species are, however, unlikely to be limited by the availability of specific food types. The Tekapo species is abundant in areas where vegetation communities are almost exclusively made up of adventive weeds, so appears to be quite an adaptable feeder.

Predation of the Tekapo wētā by introduced mammals may affect the population. Hedgehogs (*Erinaceus europaeus*) are probably the most significant mammalian predator of the wētā, followed by feral cats (*Felis catus*). Hedgehogs have populations comprising many highly mobile, nomadic individuals, making localised, occasional control ineffective. Therefore, if hedgehogs proved to be significant predators of the Cromwell wētā in places where control was feasible and justified (such as in the Cromwell Chafer Reserve), on-going hedgehog control may be warranted. It would be a relatively simple matter to establish whether or not this was the case (e.g. the examination of hedgehog faeces or stomach contents). Hedgehog control would also be to the advantage of other native ground dwelling invertebrates.

B. Recommendations.

The following is a list of recommendations for the conservation of the Cromwell *Hemiandrus* species based on conclusions drawn from the present work and from other observations of the wētā. The first two are considered the greatest priorities and the remaining recommendations are listed in approximate order of importance.

1. Clarify taxonomy.

A major research priority should be to clarify the taxonomic position of the Cromwell *Hemiandrus* species. This would best be accomplished by a formal description of the species and its closest relatives (e.g. the Tekapo *Hemiandrus* sp.).

2. Assess distribution and abundance.

Once the taxonomic status of the Cromwell species is established, and before any other conservation action is taken, the distribution and abundance of the remaining populations must be assessed. Further research into the suitability of plantation land as wētā habitat should be considered.

3. Advocacy.

Local education and publicity about the Cromwell wētā on the Cromwell Chafer Reserve would be advantageous. The reserve in the past has provided opportunities for local school students to study the ecology and conservation problems of the endangered chafer beetle *Prodontria lewisi*. In future exercises the Cromwell wētā should be considered too. This type of advocacy will increase the level of local awareness of the reserve, the wētā, and of invertebrate conservation in general.

4. Habitat enhancement.

At protected and non-protected sites where the Cromwell wētā is found to be present in viable populations, measures to maintain or enhance the soil layer should be undertaken. These should include enhancement of native vegetation by replanting suitable areas with locally derived plant species and removing grazing pressure from stock and rabbits, and the reduction or removal of fires and herbicide application (except the discriminate use of sprays to control weeds). Other land disturbance such as that from recreational motorcycles or shooters' vehicles should be discouraged.

5. Reserves.

If a reserve for the Cromwell wētā were to be established, it should be centred on an existing viable population, preferably where other natural values were high (e.g. representative natural vegetation,

perhaps including other locally or nationally threatened species). The Cromwell wētā is common on the only known area where the endangered chafer beetle *P. lewisi* is found (the Cromwell Chafer Reserve), and their habitat requirements are similar. Therefore any new reserve incorporating wētā habitat is likely to be suitable for *P. lewisi*, and if it was within the natural range of the beetle, re-introductions may be an option.

6. Monitoring the effects of management.

As recommended for the population of the beetle *Prodontria lewisi* on the Cromwell Chafer Reserve (Barratt, 1994), the population of *Hemiandrus* sp. on the reserve should be monitored with surveys at 2 - 3 year intervals to gauge the effect of reserve management on the species. Live pitfall trapping would be an appropriate low cost sampling method, even though it can lead to difficulties in correcting for differences in catch caused by variation of wētā activity over time.

7. Predator control.

A study of hedgehog diet in Cromwell wētā habitat (e.g. the Cromwell Chafer Reserve) should be undertaken to guage the local impact of these predators on the wētā. If hedgehogs are shown to be important wētā predators in areas with significant populations of Cromwell wētā, ongoing control may be justified, perhaps in conjunction with control of other mammalian predators such as cats and rodents. Removal of predator shelter and nest sites, such as large shrubs and trees (especially where these are not native) may discourage the use of these areas by predators.

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Appendices

Appendix 1. The limitations and advantages of pitfall traps.

The use of pitfall traps in ecological studies of cursorial invertebrates has been widespread for decades. Work has concentrated mostly on beetles of the family Carabidae (e.g. Mitchell, 1963; Greenslade, 1964; Ahearn, 1971; Halsall and Wratten, 1988; Luff and Eyre, 1988) and spiders (e.g. Duffey, 1962; Topping and Sunderland, 1992), although isopods (e.g. Hayes, 1970; Sunderland et al., 1976), ants (Greenslade and Greenslade, 1971) and Collembola (Joosse, 1965) have been studied. Most of these taxa are active surface moving animals and so are suited to pitfall sampling techniques.

Two major factors affect the rate of capture of animals in pitfalls (Southwood, 1978). These are:

a. the population density of the animal, and
b. the activity of the animal.

It is clear that pitfall data will not give reliable estimates of the animal's absolute abundance unless some index of activity is known (Southwood, 1978).

Topping and Sunderland (1992) clearly demonstrated the limitations of pitfall sampling. The authors compared pitfall catches of spiders with what they assumed to be an estimate of the true densities (as indicated by hand sampling of ground vegetation). Their results showed that pitfall catches did not reflect community composition. The most marked difference was that between the sexes of some spider species. Hand sampling revealed that the sexes of most species were present in roughly equal proportions, but for some, pitfalls caught up to 16 times as many males as females. This they interpreted as being caused by males being much more active while searching for mates. Additionally, the more active species were caught up to ten times as frequently in pitfalls than their actual densities would predict. Pitfall sampling will of course only represent relative abundance accurately if activity is constant between the groups being compared. This is likely to be the case where two or more sub-populations are proximal and are sampled at the same time (so that weather conditions etc. are similar).

It should be noted that other factors, especially behavioural, can affect the catch of pitfall traps. Small beetles can sometimes recover their balance after becoming unbalanced at the edge of the trap (Luff, 1975) and therefore escape. Larger beetles, with more momentum, cannot do this. Other workers (e.g. Greenslade, 1964) have noted an increased catch of larger species but attributed it simply to the larger animals covering more ground, making an encounter with a trap more likely. Hayes (1970) caught more large isopods and fewer females in his pitfalls than he determined were actually present in the beach habitat being sampled. He concluded that pitfalls were too inaccurate for this species.

The "digging-in effect" is the term given to another phenomenon associated with the use of pitfall traps (Joosse, 1965; Greenslade, 1973). When traps are established, catch rates are often very high for a short time and then decline to a roughly constant level (Greenslade, 1973). Possible explanations are the decline in population density of the target species over time, and habitat disturbance caused by setting the trap, which may initially increase activity. A simple way to reduce the latter source of error is to prepare traps earlier than needed and set them after a few days have elapsed so that the initial disturbance is over (Greenslade, 1973).

Topping and Sunderland (1992) believe that pitfalls are extensively misused in ecological studies, claiming that 40% of authors in a survey of 185 studies had used pitfall data inappropriately. Typically, workers had treated the catch as an indication of actual abundance rather than a composite of abundance and activity. However, some authors pointed out that in stable habitats, abundance changes are likely to be slow compared with those in ephemeral habitats, such as cropped fields or frequently flooded river banks. Therefore in stable habitats, activity peaks will be more noticeable.

In the present study, sampling was designed with consideration of the above problems. Traps were left in the ground continuously to minimise ground disturbance and reduce the "digging-in" effect, and were closed during non-sample periods. Sites being compared were sampled on the same nights to eliminate activity-related differences in wētā catch caused by variation in nightly weather conditions. Changes in catch over time were not considered.

It must be remembered that pitfall traps, despite their limitations, are still a very popular and useful tool for ecological studies of small cursorial animals. Their advantages are obvious. They are cheap, easy to use and can result in large catches (Halsall and Wratten, 1988). Another advantage is that they operate continuously over any desired time period, so that the catch reflects averaged activity and abundance over this time, and not those of just one point in time (Topping and Sunderland, 1992). This is a great advantage when many traps are set over a wide area.

Appendix 2. Testing the relative efficiency of "live" and "kill" pitfall traps.

Introduction.

The capture efficiencies of the "live" and "kill" pitfalls were tested under laboratory conditions. The procedure follows that of Cary (1981) with important modifications. Cary was interested in the absolute efficiency of his traps, whereas the present experiment was designed to detect any differences between the performance of two types of trap.

Methods.

One "kill" pitfall was set in the centre of a 450mm x 600mm glass fronted observation cage, and one "live" pitfall in an identical adjacent cage. A half sponge soaked in ethylene glycol was placed in the "kill" pitfall to simulate a real trap but avoid killing the experimental animals when they fell in. The other (dry) half of the sponge was placed in the "live" trap. Fifteen late instar *Hemiandrus* new sp. were maintained in separate containers, and during darkness, randomly selected individuals were introduced one at a time to each cage. Each wētā was held in a corner with a partition for ten minutes to allow it to adjust to the surroundings before being allowed to move about freely. The animals' behaviour was observed with the aid of a 15 watt red pilot light further dimmed with several layers of red cellophane (L. Field, pers. comm.). Approaches to the traps could be divided into discrete categories. The frequencies of three types of approach to the rim of the trap were recorded as follows:

1. antennae only passed over trap rim then wētā turned away,
2. antennae and any legs contacted trap rim then wētā turned away,
3. wētā fell in.

Therefore, during any approach to a trap, the maximum contact before the wētā turned away (or fell in) was recorded.

If a wētā did not immediately jump out after falling in the "kill" pitfall it was removed and washed in water to avoid poisoning with the preservative. One run of the experiment ended after 10 minutes or when one of the two wētā fell in. Each wētā was used no more than once per night. After each 15 runs, new traps were used and their positions swapped. The experiment was run a total of sixty times over 11 nights.

Results.

Wētā were highly variable in their activity once introduced into the observation enclosure; some were still and others moved about rapidly. Many specimens would continuously walk around the edges of the enclosure, thereby lessening their chances of an encounter with the trap.

There were a total of 398 approaches to the "kill" pitfall traps over 60 runs of the experiment. Of these, 233 (59%) were of type 1 (antennae only contact trap), 129 (32%) were of type 2 (antennae and legs contact trap) and 36 (9%) were of type 3 (wētā fell in) (table A2.1). Of 445 approaches to the "live" traps, 237 (53%) were type 1, 177 (40%) were type 2 and 31 (7%) were type 3 (table A2.1).

A Chi-squared test of association between the type of trap ("live" or "kill") and the type of approach (1, 2 or 3) showed no association (critical $\chi^2_{(d.f. = 2,\ \alpha = 0.05)} = 5.99$; calculated $\chi^2 = 5.36$).

Table A2.1. Frequencies of each type of approach to "kill" and "live" traps.

Type of approach ↓	Frequency of approach to trap		totals
	"kill trap"	"live trap"	
1	233	237	470
2	129	177	306
3	36	31	67
totals	398	445	843

Because the calculated χ^2 value was close to the critical value, further analysis was considered warranted. The proportions of each type of approach were compared between "kill" and "live" traps. Using Bonferroni *z* statistics, 95% "family" confidence intervals were constructed around these proportions (Neu et al., 1974; Moore, 1993). This technique can isolate any individual differences in proportions of approaches between the two treatments (Neu et al., 1974). However, as the confidence intervals of the proportions for each comparison overlap (table A2.2), there is no evidence of differences between "kill" and "live" pitfall traps for any type of approach ($\alpha = 0.05$).

Table A2.2. Proportions of each type of approach to traps, and 95% family confidence intervals (c.i.) calculated using Bonferroni *z* statistics (Neu et al., 1974).

Type of approach ↓	"kill" trap		"live" trap	
	proportion	95% c.i.	proportion	95% c.i.
1	0.586	0.527, 0.645	0.532	0.475, 0.589
2	0.324	0.268, 0.380	0.398	0.343, 0.453
3	0.090	0.056, 0.124	0.070	0.041, 0.099

On several occasions wētā were observed approaching a trap, walking over the edge, and (while

holding on to the rim with one or two legs) "exploring" the interior of the trap. These approaches always led to the wētā turning away and were recorded as type 2 approaches.

In most of the 67 approaches leading to capture the wētā was moving fast and probably unable to stop before falling in.

Discussion.

The evidence presented here suggests that "kill" and "live" pitfall traps capture wētā with equal efficiency. Only 8% of all approaches to the rim of a trap led to a wētā being caught. Cary (1981) recorded a capture rate of 32.7% with the ground wētā *Zealandosandrus gracilis* when he disguised the rims of the traps with leaf litter. However, the rate was only 3.6% when the (metal) rims were exposed and presumably detectable to wētā. The capture rate for *Hemiandrus* new sp. is very low (8%) and suggests that this species can detect the rim of the trap as it approaches. It is possible that this effect was an artifact caused by the observation light.

Additionally, Cary (1981) recorded that his wētā were twice as likely to turn away from the exposed rims after encountering them than from the disguised rims. This fact also indicates that *Z. gracilis* can detect the trap rim as it approaches.

In the present study, *Hemiandrus* new sp. appeared slightly more likely to make a close (type 2) approach to a "live" trap than a "kill" trap though the difference was not significant ($\alpha = 0.05$) (table A2.2). The possibly that *Hemiandrus* new sp. can detect the preservative in the "kill" trap, or is distinguishing between the trap types in some other way may warrant further investigation.

Appendix 3. The effect of moonlight on insect activity.

Entomologists have long believed that there is less insect activity on moonlit nights than dark nights. The first statistical study to confirm this was that by Williams (1936) who dealt with the attraction of flying insects (primarily moths of the family Noctuidae) to a light trap. He made several interesting findings. One was that those insects which show maximum activity around midnight (or the time of night when it is darkest), seem to have their activity decreased more by increasing moonlight. Those which characteristically fly at dusk and dawn show less or sometimes no lunar periodicity. Presumably these crepuscular species are not disadvantaged by extra light. Although cloud cover will cause a reduction in moonlight, Williams suggested that the increase in temperature this leads to could account for the marked increase in activity of flying insects on cloudy nights. He did, however, believe that his data showed beyond doubt that moonlight decreases catches of insects in flight.

The explanation often given for the phenomenon is that it is an avoidance mechanism by which potential prey minimise the risk of attack by visual predators (Anderson, 1966). In a study of the nocturnal activity of aquatic invertebrates, Anderson (1966) found that on nights with no moon, activity peaked just after sunset and decreased slowly over the rest of the night, while on moonlit nights, activity was similar to that during the day (i.e. minimal). In contrast, Ahearn (1971), studying five species of desert tenebrionid beetles in Arizona, U.S.A., found no decreases in surface activity with increasing moonlight. He attributed this to the alternative defences (chemical) at the disposal of these beetles.

In New Zealand some wētā are known to be most or exclusively active during moonless nights. Mercury Island tusked wētā (unnamed species) will only venture out of their burrows in pitch darkness, presumably to avoid being detected by tuatara with which they share their island home (Gibbs, 1994). The only ground wētā for which activity patterns have been monitored, *Zealandosandrus subantarcticus* form Snares Island, showed a significant activity peak around midnight (Butts, 1983).

Given the above it was considered appropriate to confine sampling in the present study to nights as close as practical to the new moon, in order to both maximise wētā catches and reduce variability of catches between sampling periods due to differences in moonlight.

Appendix 4. Plant species recorded during habitat survey.

Table A4. List of identifiable plant species divided into four groups (dicotyledons, grasses, mosses and lichens). Species in each group are arranged in approximate order of their overall recorded abundance. Ticks indicate whether a species is native or adventive, and which size class it was assigned to for the multiple regression analysis. Lichens were not included in the size classification.

Plant species	Native	Adventive	Ground cover	Inter-mediate	Large shrub
Dicotyledons					
Verbascum thapsus		✓		✓	
Rosa rubiginosa		✓			✓
Rumex acetosella		✓		✓	
Trifolium arvense		✓		✓	
Muehlenbeckia axillaris	✓		✓		
Arenaria serpillifolia		✓		✓	
Echium vulgare		✓		✓	
Sedum acre		✓	✓		
Raoulia australis	✓		✓		
Hieracium pilosella		✓	✓		
Discaria toumatou	✓				✓
Hypericum perforatum		✓		✓	
Epilobium sp.	✓			✓	
Verbascum virgatum		✓		✓	
Melicytus alpinus	✓				✓
Geranium sessiflorum	✓		✓		
Erodium cicutarium		✓		✓	
Grasses					
Bromus tectorum		✓		✓	
Poa pratensis		✓		✓	
Agrostis capillaris		✓		✓	
Carex breviculmus	✓			✓	
Vulpia bromoides		✓		✓	
Anthoxanthum odoratum		✓		✓	
Mosses					
Hypnum cupressiforme	✓		✓		
Racometrium lanuginosum	✓		✓		
Campylopus introflexus	✓		✓		
Lichens					
Neofuscelia sp.	✓				
Chondropsis semiviridis	✓				
Xanthoparmelia sp.	✓				
Cladia aggregata	✓				
Rhizocarpon geographicum	✓				